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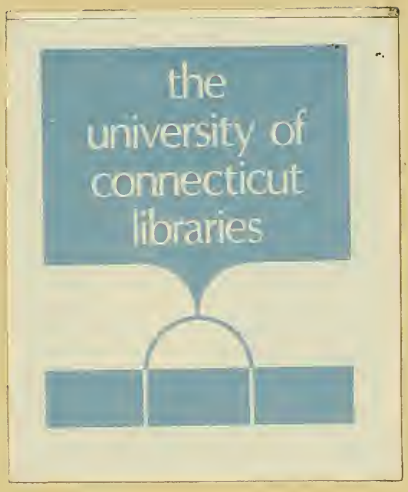

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Monograph 55

THE TITANOTHERES OF ANCIENT WYOMING, DAKOTA, AND NEBRASKA

BY

HENRY FAIRFIELD OSBORN

VOLUME 2

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UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON: 1929

Note.—Monograph 55 is issued in two volumes. Volume 1 contains Chapters I–VII and Plates I–XLII; volume 2 contains Chapters VIII–XI, Plates XLIII–CCXXXVI, an appendix, and the index to both volumes.

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CHAPTER VIII

THE MUSCULAR ANATOMY AND THE RESTORATION OF THE TITANOTHERES[49]

By William K. Gregory

SECTION 1. MUSCLES OF THE FACE AND JAW

The skeleton of Eocene titanotheres resembles that of other perissodactyls in so many points that the general position and course of the principal muscles may be inferred by comparison with the musculature of existing perissodactyls—the horses, tapirs, and rhinoceroses.

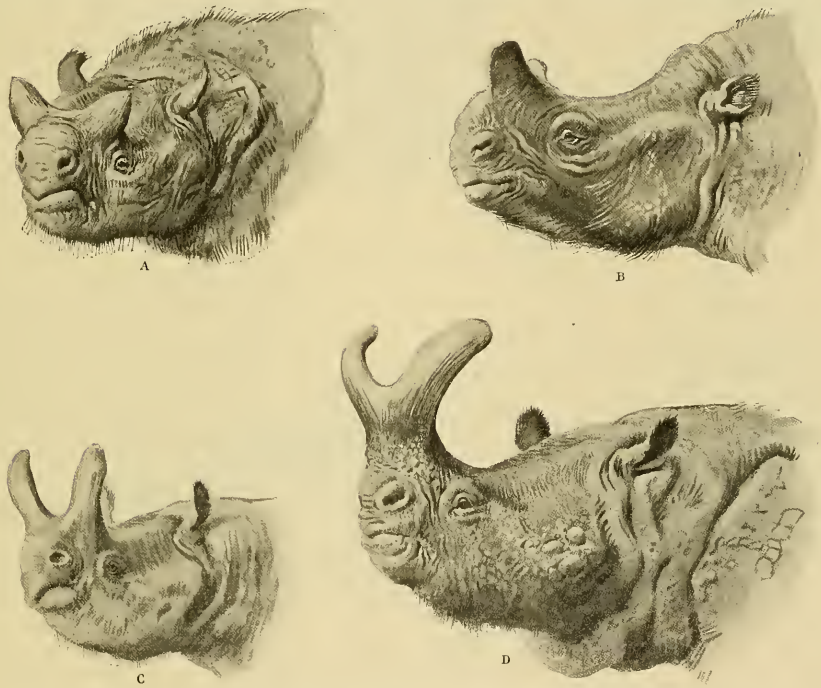


FIGURE 640.—Heads of four titanotheres

Representatives of the four principa genera of lower Oligocene time, restored by Charles R. Knight under the direction of the author. A, *Brontops robustus;* B, *Menodus giganteus;* C, *Megacerops copei;* D, *Brontotherium platyceras.* About one-seventeenth natural size.

The facial muscles of the horse, of the tapir, and of many other mammals have been described and superbly figured in a great monograph by J. F. V. Boas and S. Paulli (Boas, 1908.1). The facial muscles in the Sumatran rhinoceros have been briefly described and figured by Beddard and Treves (Beddard, 1889.1). Murie's dissection of the Malayan tapir (1872.1) and Windle and Parson's work on the muscles of the Ungulata (Windle, 1901.1, 1904.1) were also consulted. Other authorities referred to are Cuvier, Cunningham, Ellenberger, Haughton, Schmaltz, Stillman, and Weisse. (See Bibliography, p. 802.)

A study of existing musculature enabled the writer (Gregory, 1920) to infer the general anatomy of the facial muscles in the extinct Tertiary ancestors of the tapirs, horses, and rhinoceroses and especially the Eocene and Oligocene titanotheres.

In the Eocene titanotheres, such as *Manteoceras* (fig. 641), the smooth anterosuperior border of the premaxillae and the adjacent region of the maxillae, as well as the front end of the lower jaw, doubtless lay beneath the orbicularis oris muscle, which surrounded the mouth. This muscle in ungulates,

[49] The conclusions here presented are the results of studies made in 1912, 1917, and 1918 (Gregory, 1920.1). The drawings from which the figures were reproduced were made by Erwin S. Christman.

according to Boas and Paulli (1908.1), is merely the front part of the buccinator, which also extended backward alongside the grinding teeth and between the molars and the malar.

To the corner of the mouth was doubtless attached the zygomaticus muscle, which arose from the front part of the zygomatic arch, beneath the orbit.

To the surface of the upper lips at the sides was attached the wide nasolabialis, which passed obliquely upward and backward, overlying both branches of the maxillolabialis (levator labii superioris alaeque nasi), to its origin on the curved rim of the nasal and maxillary, beneath the horn swelling and in front of the orbit.

The anterior tip of the lip was raised by the superior branch of the maxillolabialis. This was perhaps joined by ligament with its fellow of the opposite side, as in the horse and tapir. It very probably ran above the huge nasal cartilage and beneath the lower rim of the nasal bone back to its origin in the wide depression in front of the orbit, which was bounded above by the nasals and behind by the raised anterior rim of the orbit.

The anterior end of the upper lip and the side of the nose were very probably retracted by the inferior branch of the maxillolabialis, which ran back along the side of the face to its tendinous origin beneath the orbital portion of the zygomatic arch. The very massive nostrils were doubtless compressed by the action of the dilator naris and lateralis nasi muscles, which surrounded the back part of the nasal chamber and its diverticulum, which together filled the space below the nasals and above the maxilla.

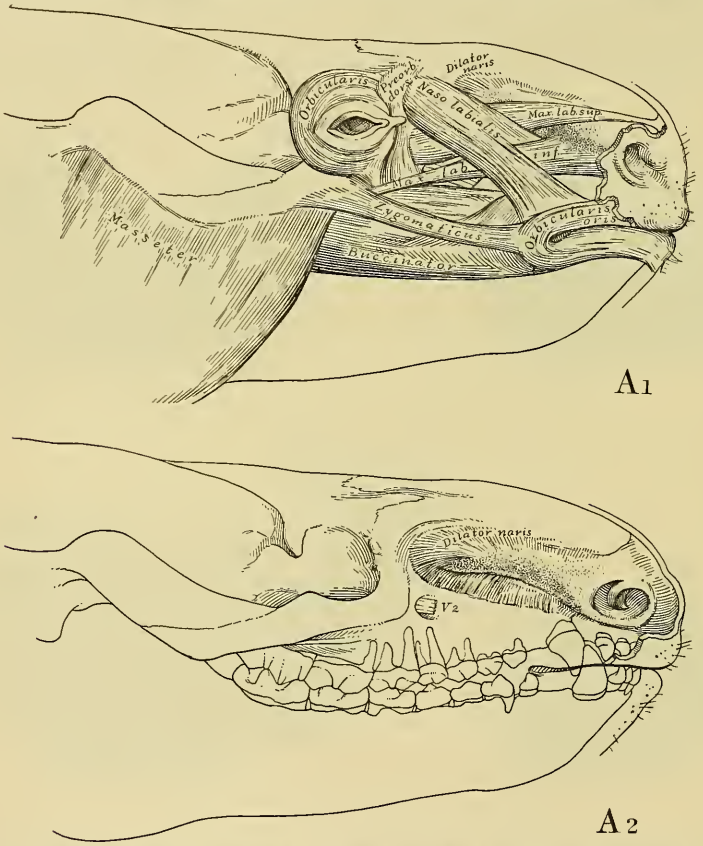


FIGURE 641.—Facial musculature and nasal cartilage of an Eocene titanothere (*Manteoceras*)

A_1, Superficial layer of muscles; A_2, relations of nasal chamber and surrounding muscles to skull. One-fourth natural size.

As thus interpreted, the Eocene titanotheres differed from the tapirs in having the upper branch of the maxillolabialis placed more directly anteroposteriorly instead of having it run more obliquely upward and forward over the nasal cartilage. This arrangement is clearly implied by the shape of the nasals which are not pointed and retracted as in the tapir but long and distally spreading. Thus the shape of the nasals in *Manteoceras* proves that this animal could not have had a proboscis. Both branches of the maxillolabialis in Eocene titanotheres probably occupied their primitive position, immediately in front of the orbit, as shown by the raised preorbital border and by the depression in front of it.

In Oligocene titanotheres the great deepening and shortening of the preorbital part of the skull was accompanied by corresponding changes in the facial muscles. The area for the nasal chamber and for the dorsal branch of the maxillolabialis was greatly increased transversely but shortened anteroposteriorly, the muscle being bounded postero-externally by the sharp external ridge running down from the horn to the front end of the zygomatic arch. The inferior branch of the maxillolabialis may well have covered the region below the infraorbital foramen, and probably its posterior tendon was attached to the rough surface below the orbital rim, along with the anterior end of the fascia of the masseter.

The progressive abbreviation of the nasals in certain phyla, *Brontops*, *Allops*, *Megacerops*, together with the great widening of the area of origin of the maxillolabialis and the narrowing of the end of the lower jaw, points to the progressive development of an enormous nasal chamber and highly protrusile lip-nostril complex of great vertical thickness.

In the *Menodus* phylum, on the other hand, the persistently wide nasals and the general configuration of the face are somewhat more suggestive of the rhinoceroses; probably these cursorial titanotheres were more square-lipped and the upper lip was less pendulous.

In Eocene titanotheres the masseter and its fascia extended over the whole lower border and part of the inner side of the malar, as indicated by the presence of deep scars in this region, analogous to similar scars among other perissodactyls. The masseter was inserted along the outer rim of the expanded angle of the mandible.

In Oligocene titanotheres the masseter was relatively of enormous size. The temporal muscle doubtless filled a great part of the temporal fossa and was inserted on the rather small coronoid process. The internal and external pterygoids were as well developed as in other perissodactyls. They doubtless assisted greatly in oblique and lateral movements of the mandible in feeding.

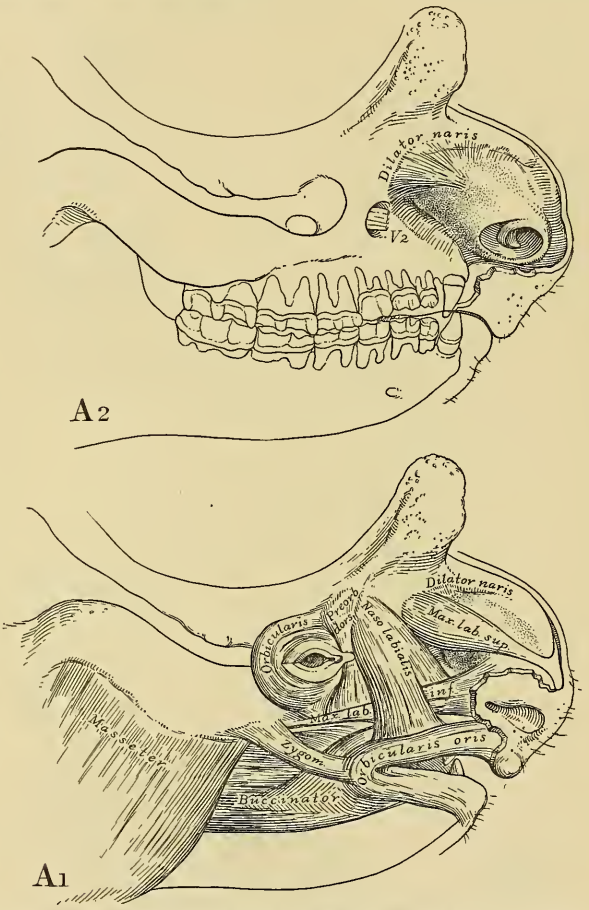


FIGURE 642.—Facial musculature and nasal cartilage of a lower Oligocene titanothere (*Menodus giganteus*)

A_1, Superficial layer of muscles; A_2, relations of nasal chamber and surrounding muscles to skull. One-sixth natural size.

SECTION 2. RESTORATIONS OF THE HEADS OF TITANOTHERES

Preliminary restorations of the heads of a series of eight Eocene and Oligocene titanotheres were made some years ago by Charles R. Knight under the direction of Professor Osborn (figs. 220, 640). Afterward it was felt that the mouth and nose of these models called for further study, and a series of life-size head models was projected.

In preparation for this work and as a part of our studies of the muscular anatomy of the entire titanothere skeleton, Gregory and Christman made a comparative study of the head muscles of the tapir, horse, elephant, and other mammals, as elaborately figured by Boas, Murie, Schmaltz, and others. Observations were also made of freshly dissected heads of horses and zebras. The correlations between bone form, muscle form, and external appearance were observed not only by this means but in living rhinoceroses, tapirs, and other animals in the New York Zoological Park and elsewhere. These observations were gradually applied to the study of the muscular anatomy of the heads of titanotheres; and the probable location of the bony areas of muscular origin and insertion were determined and illustrated in the series of diagrams here presented.

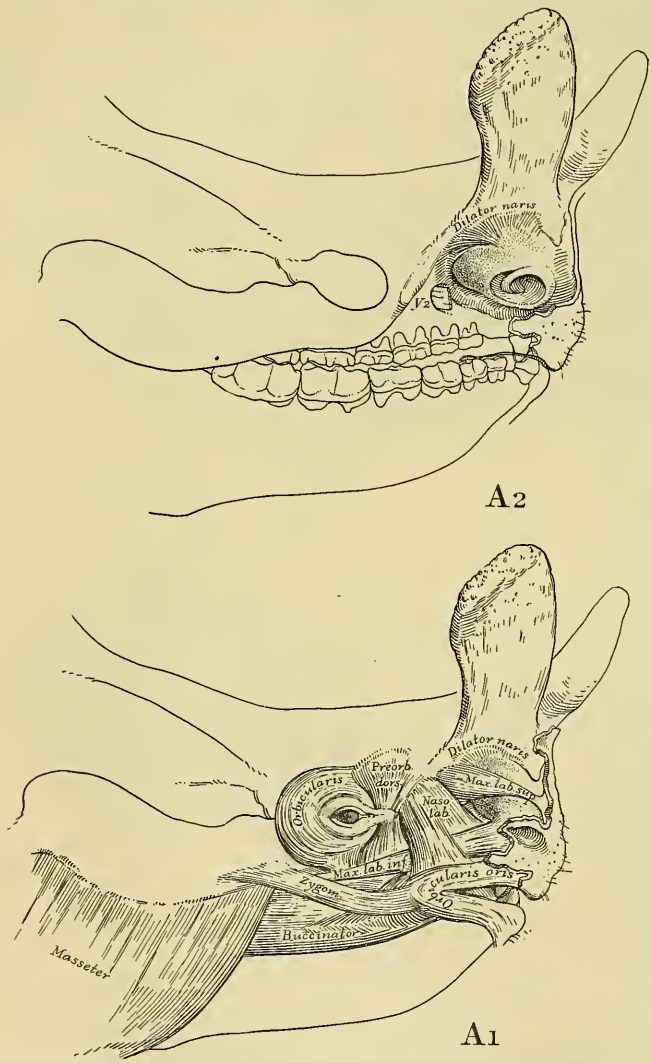


FIGURE 643.—Facial musculature and nasal cartilage of a lower Oligocene titanothere (*Brontotherium platyceras*)

A1, Superficial layer of muscles; A2, relations of nasal chamber and surrounding muscles to skull. One-sixth natural size.

Next a series of reconstructions of the skulls of five Eocene and Oligocene titanotheres was carefully made. Each model in this series forms a synthesis of the best-preserved specimens of parts of the skull of the species it represents, for no one fossil skull is perfectly preserved. In these models also the distortion and crushing of the originals were corrected. The muscles of the jaw, neck, and face were modeled first upon one side, and after the models had been photographed in this stage the other side was modeled.

The general shape of the muscles of the jaw and neck in recent perissodactyls is plainly indicated by the form and extent of the temporal fossae, lower jaw, and occiput, and our models of titanothere heads are doubtless fairly accurate in these parts. The precise shape of the nose and lips is more difficult to determine, but the models here figured represent the result of a series of carefully considered hypotheses based upon a wide range of comparative anatomical facts.

In this series of restorations we have taken into account the origin, evolutionary trend, and systematic relations of all the animals studied. First we considered the structure, the habits, and the probable appearance of the earliest known and generalized members of the titanothere group and of the related families of perissodactyls—the earliest "tapirs," "rhinoceroses," "horses," etc. Second we studied the diverse and highly specialized end members of these families, and third we studied the intermediate types. In the order Perissodactyla unusually complete material for such study is available. We know the skull and the dentition of many genera of primitive lower Eocene perissodactyls; we know the features of a still greater number of their divergent descendants in the middle

and later Tertiary; and we still have surviving the very diversely specialized end members of three families—the tapirs, rhinoceroses, and horses. The divergent trends of evolution in food habits and structure from the primitive Eocene perissodactyls to their latest descendants are accordingly fairly well known, and we have attempted to illustrate them in the series of restorations of Eocene and later perissodactyls shown in Chapter IX.

These divergent trends of evolution in the perissodactyls are especially evident in the region of the nostrils and lips. In the earliest true titanothere, *Eotitanops*, the incisor and canine teeth and the whole front part of the jaws differed only in minor characters from the same parts in the contemporary primitive tapirs, rhinoceroses, and horses. Our restoration of the head of *Eotitanops* resembles our previous

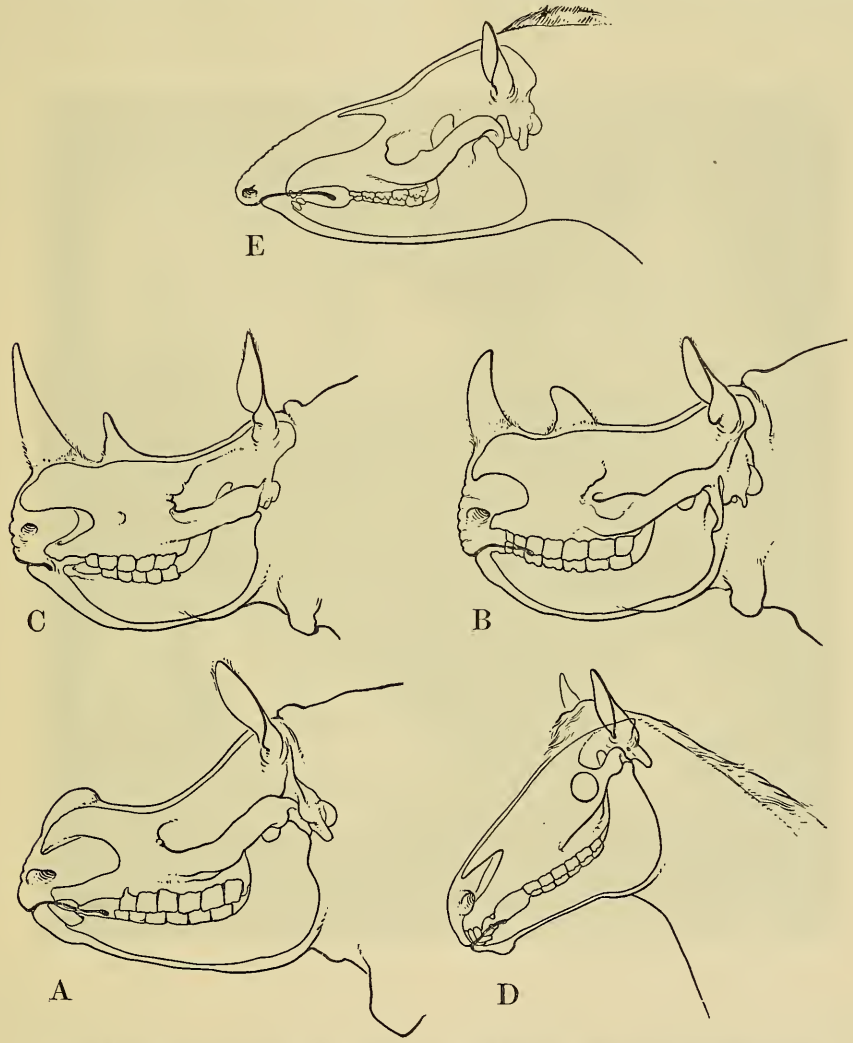


FIGURE 644.—Relation of the contour of the head to the skull and jaws in living perissodactyls

A, *Rhineroceros indicus* (Indian rhinoceros); B, *Opsiceros bicornis* (black rhinoceros); C, *Ceratotherium simum* (white rhinoceros); D, *Equus* (horse); E, *Tapirus terrestris* (tapir). In E the restriction of the nasals is associated with a marked outgrowth of the protrusile proboscis. The angle of the mouth usually extends behind the anterior premolars, but in some species, as in the white rhinoceros, it is in front of the tooth row. The nostrils are generally in line with the middle of the narial sinus.

restorations of the head of the earliest "horse" (*Eohippus*) and of the earliest cursorial "rhinoceros" (*Hyrachyus*), because the skulls themselves show an underlying similarity. However, as the incisors, canines, and bony jaws of *Eotitanops* already exhibit a step toward those of the titanotheres of the later Eocene, we felt justified in making the muzzle and lips heavier than those of the contemporary horses.

FIGURE 645.—Model of half of skull and head of an Eocene titanothere (*Palaeosyops leidyi*)
Modeled by E. S. Christman under the direction of William K. Gregory. About one-eighth natural size.

In the middle Eocene *Palaeosyops* (fig. 645) the structure of the jaws and the nasal region, in comparison with those of tapirs and horses, gives very definite evidence that the nostrils were nearly terminal and the muzzle partly protrusile.

The restoration of the muzzle and lips of the final member of the brontothere phylum, namely, *Brontotherium platyceras*, was more difficult. The hypothesis that this kind of titanothere had a proboscis lip is improbable, because the entire front part of the skull is widely different from those of tapirs and elephants. If *Brontotherium* had any form of proboscis we should expect to find that the fossae for the origin of the levator muscles of the nose and lips and for the nasal chamber would be either more tapiroid or more elephantine in form than they are. The head seems to have been carried so low that a heavy, square, protrusile muzzle, rather than a true proboscis, would be sufficiently long to reach the ground.

As noted above, the extreme and abrupt narrowing of the nasal tips in the advanced stages of *Brontotherium* and the expansion of the areas for the muscles of the nose and lips seem to indicate that the muzzle of these animals was very large and that the lips were extremely muscular, thick, and protrusile—not at all proboscis-like but more like those of the black rhi-

noceroses. The construction of the jaws and grinding teeth indicates that their main food was very coarse herbage, rather than grass, so it is reasonable to suppose that the mobile lips would be adapted rather to browsing and tearing up shrubs than to cropping short grass, and consequently that the median part of the lips would be pointed and very protrusile, somewhat as in the black rhinoceros, rather than truncate, as in the grazing lips of the white rhinoceros and horse.

Such being our conceptions of the first and of the last known members of the family, it seems reasonable to assign the middle Eocene genus *Manteoceras* (in which the bones and teeth were structurally intermediate between these extremes) to an intermediate stage in the development of the nose and lips (figs. 646–649).

The restoration of the fore part of the head of the upper Eocene *Protitanotherium emarginatum* is based upon the well-preserved facial bones and lower jaw of the type and is probably fairly accurate, but the restoration of the back part of the head is hypothetical.

In Figure 647 we give another series of restorations, showing the heads of members of the principal genera of middle and upper Eocene titanotheres, except the Palaeosyopinae, and showing also the contour of the skull.

SECTION 3. MUSCLES OF THE NECK AND BACK

In the following pages we have attempted to determine what muscles and ligaments were attached to the principal parts of the skeleton; hence the subject matter is classified primarily according to the topography of the skeleton, secondarily according to musculature.

The vertebrae of titanotheres are sufficiently like those of the horse to indicate that the axial musculature was also essentially similar. The following description is based largely on Schmaltz's (1909.1) figures of the cervical and dorsal musculature of the horse supplemented from photographs by Herbert Lang of a dissected white rhinoceros.

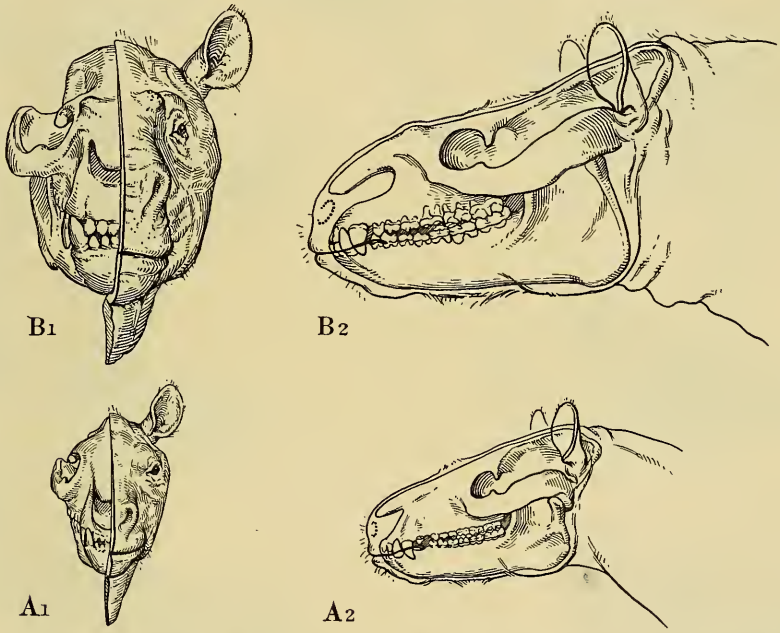


FIGURE 646.—Models of half of the skull and head of *Eotitanops borealis* (A) and *Manteoceras manteoceras* (B)

Modeled by E. S. Christman under the direction of William K. Gregory. One-eighth natural size.

The occiput (fig. 650), especially in the later titanotheres, bore highly rugose crests, which probably separated the jaw muscles (temporals) from the neck muscles and were covered with thick, tough skin. A deep median pit marks the insertion of the ligamentum nuchae. The semispinalis capitis (complexus) was probably inserted just beneath the occipital crest and lateral to the ligamentum nuchae. The splenius was lateral to the semispinalis and probably formed a wide sheet just behind the lateral occipital ridge. Below the splenius and behind the auditory meatus was the insertion for the tendon of the longissimus

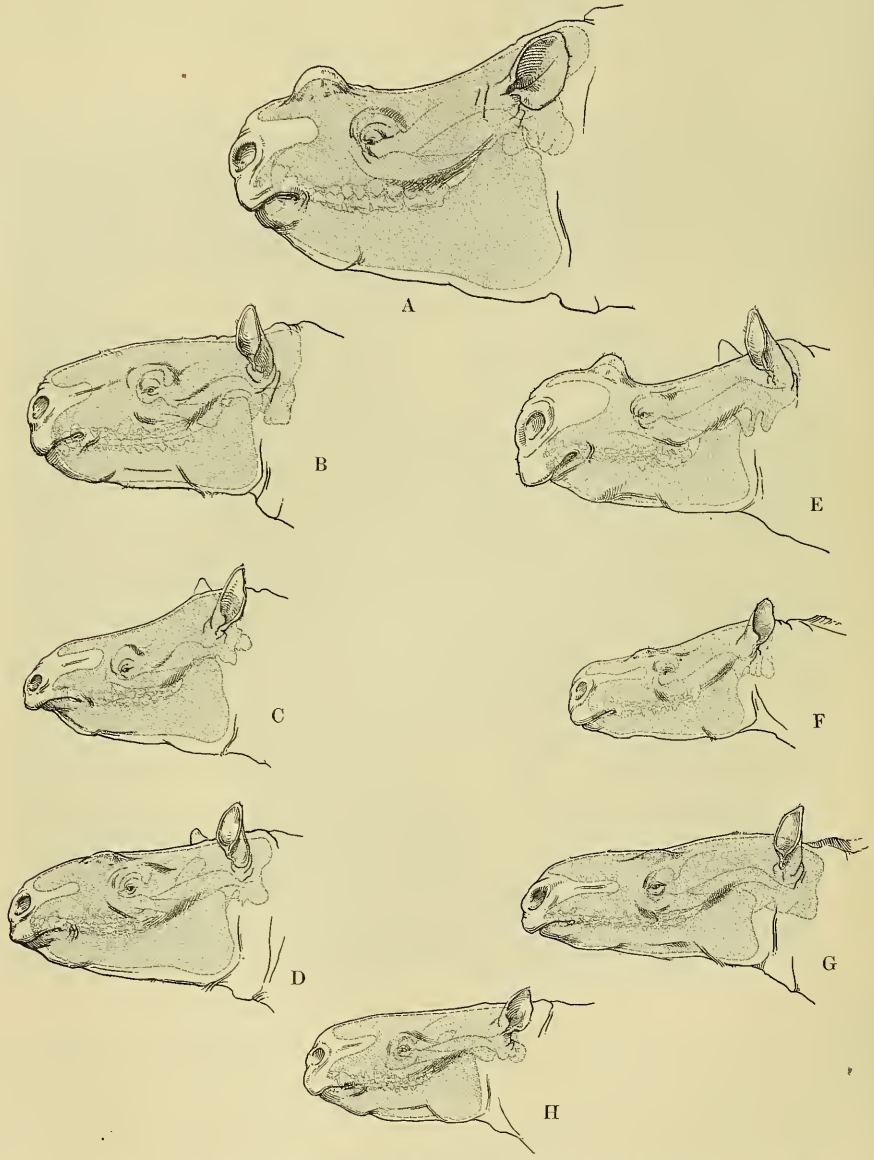


FIGURE 647.—Heads of titanotheres belonging to eight genera of middle and upper Eocene time

Restored in accordance with the skull contours by Mrs. E. M. Fulda under the direction of William K. Gregory. A, *Protitanotherium superbum;* B, *Telmatherium ultimum;* C, *Rhadinorhinus diploconus;* D, *Manteoceras manteoceras;* E, *Eotitanotherium osborni;* F, *Metarhinus earlei;* G, *Dolichorhinus hyognathus;* H, *Mesatirhinus petersoni.* One-twelfth natural size.

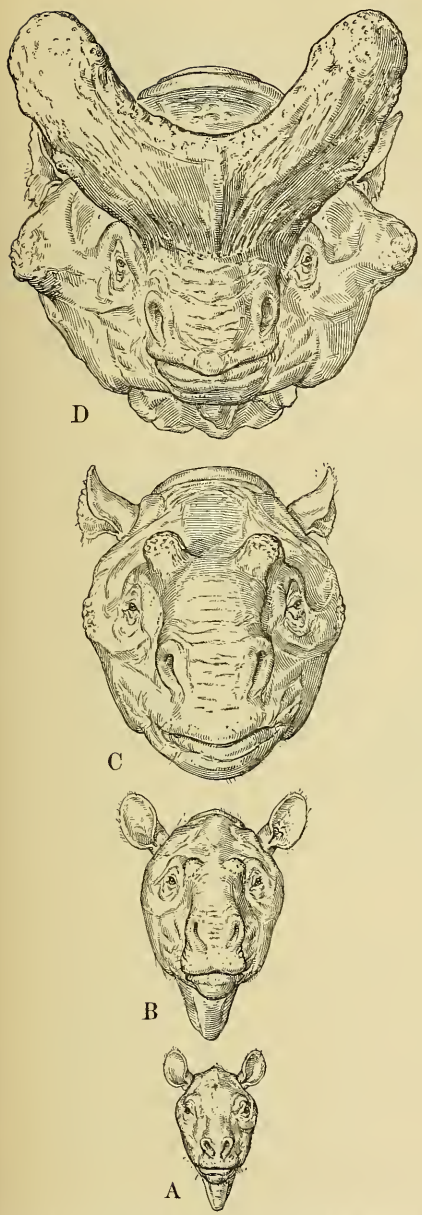


FIGURE 648.—Heads of four titanotheres, showing progressive stages of development

Front view. Modeled and drawn by E. S. Christman under the direction of William K. Gregory and H. F. Osborn. A, *Eotitanops borealis*, lower Eocene; B, *Manteoceras manteoceras*, middle Eocene; C, *Protitanotherium emarginatum*, upper Eocene; D, *Brontotherium platyceras*, lower Oligocene. One-ninth natural size.

FIGURE 649.—Heads of four titanotheres, showing progressive stages of development

Side view. Modeled and drawn by E. S. Christman under the direction of William K. Gregory and H. F. Osborn. H, *Eotitanops borealis*, lower Eocene; G, *Manteoceras manteoceras*, middle Eocene; F, *Protitanotherium emarginatum*, upper Eocene; E, *Brontotherium platyceras*, lower Oligocene. One-twelfth natural size.

capitis, and below this in turn, near the lower end of the mastoid process, was the insertion of the tendon of the cephalohumeralis (cleidomastoideus). Beneath the semispinalis and splenius is a wide nuchal surface for the obliquus capitis superior, rectus posticus major, and rectus posticus minor. The relations of all these muscles to the cervical vertebrae are shown in Plate XLIII.

The rugose tips of the dorsal and cervical spines served for the origin of the ligamentum supraspinale and the ligamentum nuchae, the latter being inserted into the tips of the cervical vertebrae and into the to the longissimus atlantis. Both had short branches arising from the outer surface of the prezygapophyses of successive vertebrae. Below the zygapophyses and above the transverse processes were the intertransversarii muscles, which also extended from one transverse process to the next. The outer rugosity of the transverse processes also bore the slips of the scalenus brevis (primae costae), levator scapulae ("serratus cervicis"), and cephalohumeralis.

The infero-anterior processes of the cervical vertebrae gave rise to slips of the longus colli, which, joining with similar slips from the inferior faces of the centra,

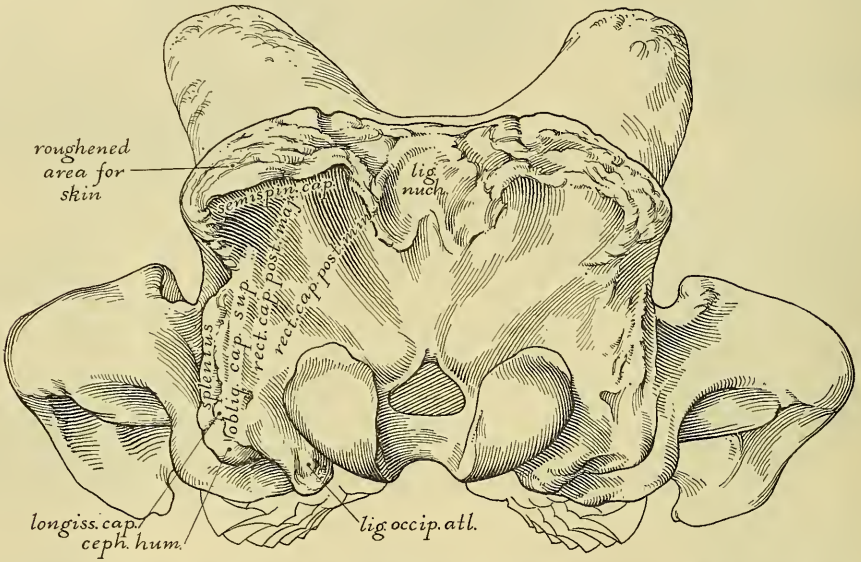


FIGURE 650.—Occiput of an Oligocene titanothere (*Brontops robustus*), showing the probable general location and planes of the neck muscles

The extremely rough occipital and lambdoidal crests were probably covered with tough skin, as in recent perissodactyls. The precise limits of the insertion areas can not be determined. Two-ninths natural size.

middle of the occiput (fig. 650). On the anterior edges of the neural spines of the cervicals were inserted the slips of the spinalis dorsi (cervicis). The sides of the cervical spines carried the multifidus spinae, which ran obliquely downward and backward to be inserted above the posterior zygapophyses of the next succeeding vertebrae. The outer dorsal rims of the postzygapophyses bore the slips of the semispinalis capitis, which ran upward and forward, converging toward and being inserted on to the nuchal surface, just below the occipital crest and on either side of the midline (fig. 650). Along the line of the prezygapophyses and postzygapophyses ran both the longissimus capitis, which was inserted into the posterolateral margin of the lambdoidal crest behind the auditory meatus, and the longissimus atlantis, which was inserted into the edge of the transverse process of the atlas. The longissimus capitis lay immediately dorsal ran forward and were inserted on the hypapophysis of the atlas.

The principal attachments of the muscles and ligaments of the presacral vertebrae are summarized below. It is assumed that every homologous part in the horse and the titanothere would carry a homologous muscle and ligament attachment. The very full data for such attachments in the modern horse given by Schmaltz (1909.1) accordingly form the chief basis of the determinations given.

Principal attachments of the muscles and ligaments in the presacral vertebrae in the horse and the titanothere

Muscle attachments of the atlas. (See Pl. XLIII)

Neural spine (s): rectus capitis posticus minor.
Transverse process (t), dorsal surface: obliquus capitis inferior.
Transverse process (t), ventral surface: obliquus capitis superior.
Transverse process (t), external border: obliquus capitis superior.

Transverse process (t), posterior border: longissimus atlantis.
Inferior median spine: longus colli.
Inferior arch, ventral surface: rectus capitis anticus lateralis, rectus capitis anticus minor.

Ligament attachments of the atlas

Inferior arch: ligamentum occipito-atloideum ventrale.
Superior arch: ligamentum occipito-atloideum dorsale.

Muscle attachments of the axis. (See Pl. XLIII)

Neural spine, median line: rectus capitis posticus major et medius.
Neural spine, lateral surface: obliquus capitis inferior.
Neural spine, lateral surface, posteriorly: multifidus spinae.
Postzygapophysis, dorsal surface: semispinalis capitis (complexus).
Base of neural arch, side of centrum, and posterior portion of transverse process: intertransversales.
Transverse process, posteriorly: cleidomastoideus.
Inferior median keel, laterally: longus colli.

Ligament attachments of the axis

Neural crest, posteriorly: ligamentum nuchae.
Neural spine, anteriorly: ligamentum interspinale.
Neural arch, anterior border: ligamentum atlo-axoideum dorsale.
Odontoid process, anteriorly: ligamentum apicis dentis.
Centrum, inferiorly: ligamentum atlo-axoideum ventrale.

Muscle attachments of cervical vertebrae

Neural spine, anterolaterally: spinalis dorsi et cervicis.
Neural spine, posterolaterally: multifidus spinae.
Prezygapophysis and postzygapophysis, superficially: semispinalis capitis (complexus).
Prezygapophysis and postzygapophysis, middle layer: longissimus capitis et longus atlantis.
Prezygapophysis and postzygapophysis, deep layer, superior: multifidus spinae.
Prezygapophysis and postzygapophysis, deep layer, inferior: intertransversales.
Pedicle of neural arch above transverse process: intertransversales.
Transverse process, antero-inferior ventral surface: longus colli.
Transverse process, posterosuperior: intertransversales, longissimus cervicis, scalenus costarum, serratus anterior, rectus capitis anticus major, cleidomastoideus, splenius capitis.
Inferior spine, laterally: longus colli.

Ligament attachments of cervical vertebrae

Neural spine, tip: ligamentum nuchae.
Neural spine, anterior median: ligamentum interspinale.
Neural spine, posterior median: ligamentum interspinale.
Neural arch, laterosuperiorly: ligamentum subflavum.
Centra, dorsally, forming floor of neural canal: ligamentum commune dorsale.
Centra, ventrally: ligamentum commune ventrale.

Muscle attachments of second dorsal vertebra. (See fig. 651)

Neural spines, near summit, laterally: splenius capitis, semispinalis capitis (complexus).
Neural spines, anterolaterally: spinalis dorsi et cervicis.
Neural spines, posterolaterally, upper part: spinalis dorsi.
Neural spines, posterolaterally, lower part: multifidus spinae.
Transverse process, dorso-externally: semispinalis capitis, multifidus spinae, longissimus cervicis, longissimus dorsi, levator costae.

Ligament attachments of second dorsal vertebra

Similar to those of the cervical vertebrae (see above); also on tip of neural spine: ligamentum supraspinale

Muscle attachments of tenth dorsal vertebra.

Neural spine, near tip: spinalis dorsi or longissimus dorsi.
Neural spine, posterolaterally: multifidus spinae.
Transverse process, dorsal: multifidus spinae, longissimus dorsi, levator costae.

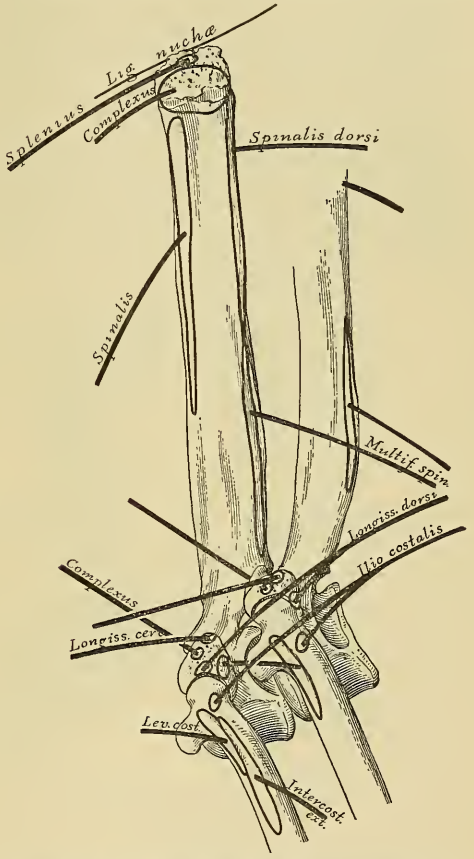


FIGURE 651.—Probable position and attachments of the principal muscles of the second and third dorsal vertebrae of a lower Oligocene titanothere (*Brontops* cf. *B. robustus*)

Insertion areas in thinner black lines; directions of muscles in heavy black lines. One-eighth natural size.

Ligament attachments of tenth dorsal vertebra

[See Pl. CXCIX]

Muscle attachments of second lumbar vertebra

Neural spine, on either side of tip: longissimus dorsi.
Neural spine, posterolaterally: multifidus spinae.
Prezygapophysis, antero-externally: multifidus spinae.
Side of centrum concealed by psoas minor.

Ligament attachments of second lumbar vertebra

Chief ligaments as in preceding vertebrae; also, to postero-external corner of centrum: ligamentum iliolumbale.

SECTION 4. MUSCLES OF THE LIMBS OF THE EOCENE TITANOTHERE PALAEOSYOPS (SUBGRAVIPORTAL TYPE)

The limb bones of the middle Eocene titanothere *Palaeosyops* are so much like those of existing tapirs (*Tapirus*) that it is highly probable that the positions and courses of the muscles were also essentially similar, the differences being chiefly due to the more robust development of certain muscles in *Palaeosyops*. Both animals are tetradactyl-tridactyl. *Tapirus* is typically mediportal; *Palaeosyops* is subgraviportal.

In the following study Murie's description (1872.1) of the myology of the tapir and Windle and Parson's studies (1901.1; 1903.1) on the muscles of the ungulates were constantly used, and comparisons were made with the myology of other mammals, especially the horse, as figured by Schmaltz (1909.1).

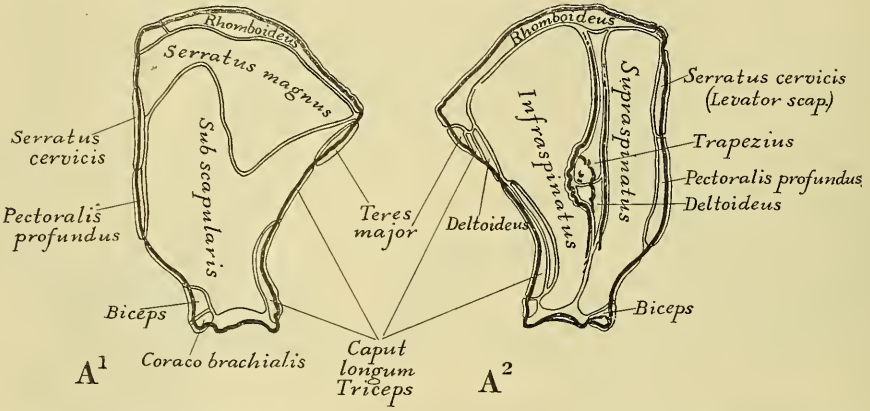


FIGURE 652.—Right scapula of a lower Oligocene titanothere (*Brontotherium* cf. *B. gigas*), showing the principal muscle attachments

A1, inner side; A2, outer side. (Compare fig. 623.)

MUSCLES OF THE FORE LIMB

[See Pl. XLIV, A]

MUSCULAR ATTACHMENTS OF THE SCAPULA

The large scapula is about $\frac{91}{100}$ as long as the humerus and afforded a broad base for the massive shoulder muscles. The superior border is roughened for the rhomboideus; the anterosuperior continuation of this roughening may have given attachment to the serratus cervicis (levator scapulae) subclavius and, in its antero-inferior part, to the pectoralis profundus (pars ascendens).

The coracoid process gave origin anteriorly to the single-headed biceps and inferiorly to the coracobrachialis.

The supraspinous fossa and its muscle area for the supraspinatus are broad and well defined, and the same is true of the postspinous fossa, which is the area chiefly for the infraspinatus. The spine of the scapula is reflected and bears a prominent tuberosity for the tendon of the trapezius, which covered the deep shoulder muscles of the neck and back. To the lower border of the spine was attached a slip of the deltoid, which lay outside the broad infraspinatus muscle.

The infraspinatus muscle passed downward below the spine and above the teres minor, which in turn was probably attached to the ridge for the teres minor, obliquely traversing the lower third of the postspinous fossa. Above and behind this streak, near the angle of the scapula, is a rough streak which is probably for a second slip of the deltoid.

Along the axillary border and running below into a rugose axillary prominence, as well as into a curved area behind the ridge for the teres minor, is the origin of the long head of the triceps, the largest muscle of the forearm. The posterior angle of the scapula is roughened for the teres major.

The medial or internal surface of the scapula in its upper third bears a large triangular roughening for the serratus magnus; below this nearly the whole surface was filled by the subscapularis.

Near the axillary border the medial surface is raised into a long, gently convex eminence or column running parallel and internal to the postspinous fossa and culminating above in the surface for the serratus. This subscapular column greatly strengthens the blade against the pull of the serratus, infraspinatus, subscapularis, and caput longum of the triceps.

MUSCULAR ATTACHMENTS OF THE HUMERUS

The great tuberosity, expanded into a broad flange, gives insertion on its anterior hook to the supraspinatus; a branch of this muscle forks over the biceps and is inserted into the lesser tuberosity. The superior and external surfaces of the great tuberosity form the insertion area for the infraspinatus. The bicipital groove is filled by the single-headed biceps.

The high deltopectoral crest gives attachment to the teres minor and below this is produced into a large reflected protuberance for the deltoid. The rough anterior border of the deltopectoral crest probably gave origin for a branch of the cephalohumeralis. Windle and Parsons (1901.1, p. 679) state that this muscle is a combination of the anterior part of the trapezius, the cleidomastoid, and the clavicular part of the deltoid.

The lower extension of the deltopectoral crest very probably gave attachment to the pectoralis superficialis (p. major) and below this to the cephalohumeralis. The posterior upper border of the deltopectoral crest probably gave attachment to the external head of the triceps.

behind and below it was attached the medial head of the triceps.

From the entocondyle arose the medial or humeroradial collateral ligament and the several flexors of the forearm.

Above the olecranal fossa is an area which was probably for the so-called anconeus; this muscle in ungulates appears to represent a fourth head of the triceps.

MUSCULAR ATTACHMENTS OF THE RADIUS

The head of the radius was flattened and appressed to the ulna, and the radio-ulnar facets permitted only a very slight degree of supination. In correlation with this the tubercle (fig. 654, tub.) was greatly reduced and no longer served as the chief insertion

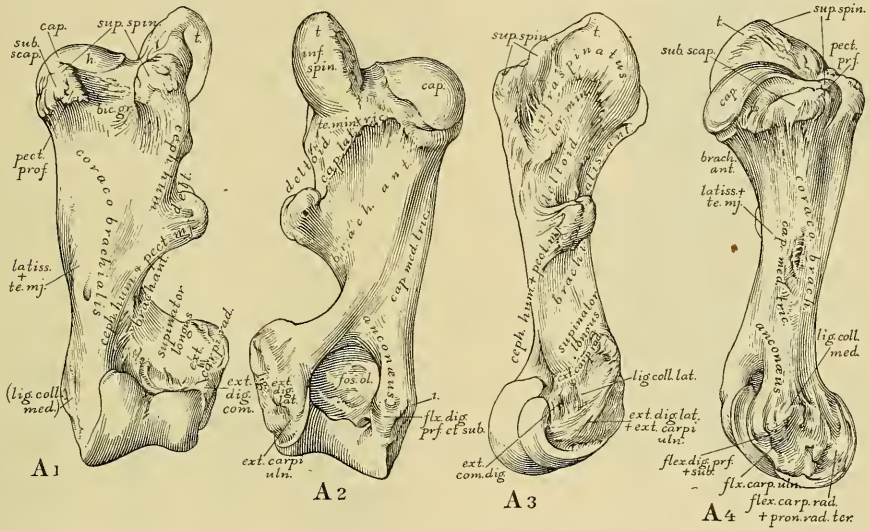


FIGURE 653.—Left humerus of *Brontops robustus* (type), showing probable position and attachments of principal muscles

A_1 Front view; A_2, back view; A_3, outer side view; A_4, inner side view. One-eighth natural size.

The extensive winding surface for the brachialis anticus on the back of the humerus passes from above downward and forward; it lies behind the deltoid crest. Below the brachialis anticus area and above the supinator crest arose the powerful supinator longus and extensor carpi radialis.

From the region of the ectocondyle arose the humeral slip of the extensor communis digitorum, the external collateral ligament, and the extensor carpi ulnaris, which in ungulates serves as a flexor of the forearm.

On the inner or costal side of the humerus we observe especially the attachment for the subscapularis (into the lesser tuberosity) and the latissimus rugosity for the common tendon of the teres major and latissimus dorsi. Below and in front of the latissimus rugosity is the insertion area for the coracobrachialis, while

point for the tendon of the biceps; this tendon was probably inserted chiefly on the front of the head of the radius and may also have extended around to the inner side, as in *Tapirus* and *Equus*.

On the inner or medial surface of the radius about 2 inches below the proximal end is a rugose area which is probably for the insertion of the medial collateral ligament. Below this, in the middle third of the shaft and partly on the front surface, is a vertically extended rugosity which was probably, as in *Rhinoceros*, the attachment area of the brachialis anticus. At first sight the rugosity in question seemed to be for the pronator radii teres, as in carnivores, but in the tapir and apparently also in *Palaeosyops* the tendon of this muscle extended down the whole inner edge of the radius. (Murie, 1872.1; Turner, 1850.1.)

MUSCULAR ATTACHMENTS OF THE ULNA

The massive olecranon has a very rough area for the long head of the triceps; to the olecranon were also attached the external (lateral) and medial (internal) heads of the triceps, also the fourth head, or "anconeus." The inner side of the olecranon probably gave attachment to the palmaris longus and to branches of the flexor digitorum profundus and flexor carpi ulnaris.

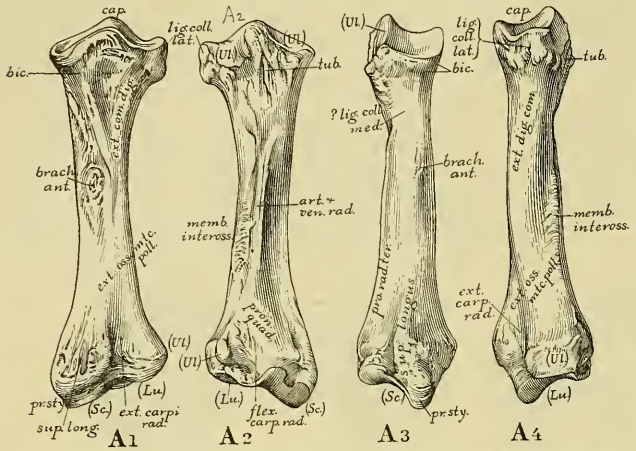


FIGURE 654.—Left radius of *Brontops robustus* (type), showing probable position and attachments of principal muscles

A1, Front view; A2, back view; A3, inner side view; A4, outer side view. One eighth natural size.

The antero-external face of the ulna, together with the adjacent side of the radius, probably lodged the extensor ossis metacarpi pollicis (extensor metacarpi obliquus), and the rough outer border of the ulna may have been for a slip of the extensor communis digitorum.

The lower end of the ulna, closely appressed to the radius, retained but little independent movement, yet more than in the tapir. To the outer side of the shaft near the lower end was attached the lateral ulnocarpal ligament. Possibly the groove near the end of the ulna, above the cuneiform, lodged the tendon of the extensor digitorum lateralis.

On the antero-internal edge (or interosseous ridge) of the ulna was stretched the strong interosseous membrane which separated the extensor from the flexor surfaces of the forearm.

MUSCULAR ATTACHMENTS OF THE CARPUS

The proximal row of carpals, like those of *Equus*, was bound together transversely by a series of ligaments running across the front face of the carpus and connecting respectively with the inner and outer distal portions of the radius. The distal row of carpals was similarly bound together by a second series of ligaments so that during flexion the proximal and distal rows moved apart vertically but preserved their transverse alinement.

On the posterior aspect of the carpus the pisiform gave insertion superiorly to the flexor carpi ulnaris and possibly also to a slip of the extensor carpi ulnaris, inferiorly to the abductor minimi digiti; it was also no doubt embraced by the annular ligament. The extensor carpi ulnaris, according to Windle and Parsons (1901.1, p. 700), in most ungulates serves as a powerful flexor of the carpus. According to these authorities the slip attached to the pisiform (which appears to the present writer to belong rather to the true flexor carpi ulnaris) is present in *Equus* and many artiodactyls but is barely or not at all developed in *Tapirus, Rhinoceros, Hyrax, Elephas, Canis, Homo.* Hence this pisiform slip may also have been absent in *Palaeosyops.*

The tuberosities on the posterior aspect of the carpus gave attachment for a set of ligaments radiating from the middle bones (lunar, magnum) to the surrounding elements. The posterior tuberosity of the lunar also gave attachment to the interosseus dorsalis primus, abductor minimi digiti, and adductor minimi digiti. The posterior tuberosity of the magnum, the form of which is very characteristic of perissodactyls, gave attachment not only to the radiating ligaments

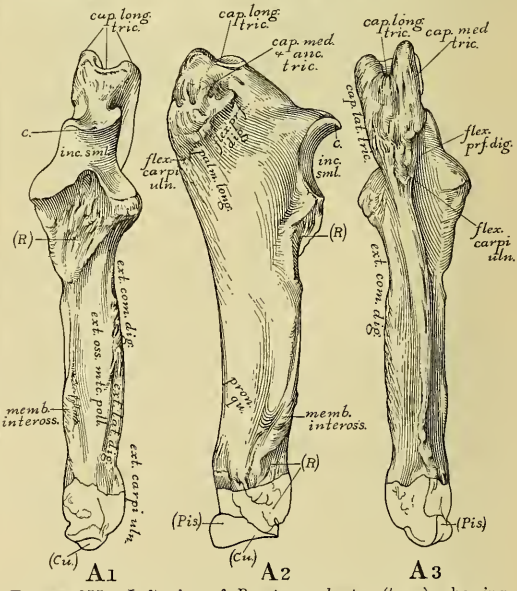


FIGURE 655.—Left ulna of *Brontops robustus* (type), showing probable position and attachments of principal muscles

A1, Front view; A2, inner side view; A3, back view. One-eighth natural size.

above mentioned, but also to the adductor minimi digiti, the adductor indicis, and the adductores digitorum medii et quarti. The spaces between the proximal ends of adjacent metacarpals gave rise to the dorsal interossei, while the depressions on the posterior aspect of the proximal portion of the metacarpals served for the origin of the palmar interossei which were inserted into the sesamoids, the latter being attached by ligaments to the proximal phalanges. The inner and outer sides of the metacarpals show distally deep lateral pits, one on either side of the facets for the phalanges; these pits were for the collateral ligaments that passed to the first row of phalanges and were inserted on their proximal inner and outer expansions.

The palmar surfaces of the first row of phalanges were covered by the flexor digitorum profundus. The lateral protuberances at the proximal ends probably served for the collateral ligaments, while pairs of proximal palmar rugosities probably served for the ligaments of the sesamoids. At the sides of the proximal phalanges may have been attached the adductors of the digits and the lumbricales (accessory flexors arising from the tendon of the flexor sublimis). Toward the distal end the lateral pits were probably for the collateral ligaments, while the protuberances above them probably gave attachment to the flexor sublimus.

The second row of phalanges (fig. 656) gave insertion to the forked flexor profundus in the midpalmar surface. The dorsal surface of the second phalanges gave insertion to the extensors of the digits. The distal or ungual phalanges gave insertion on their dorsal surfaces to the extensors and on their palmar surfaces to the flexor sublimis. The distal roughening for the hoof indicates a relatively small hoof in comparison with the tapir and rhinoceros.

The whole palmar surface of the manus was probably covered superficially by the flexor brevis manus, as in the tapir.

MUSCLES OF THE HIND LIMB

[See Pl. XLIV, B]

MUSCULAR ATTACHMENTS OF THE SACRUM

The sacrum was securely fastened to the ilium by a system of iliosacral ligaments probably similar in essentials to those in *Equus* as figured by Schmaltz (1909.1, Taf. 6) and consisting of (1) a dorsal ligament (called by Schmaltz the ligamentum sacro-iliacum dorsale breve) running along the tips of the sacral spines and being inserted anteriorly into the dorsal border of the sacral flange of the ilium; (2) a broad ligament running from the lateral edge of the transverse lamina of the sacrum obliquely upward and forward to the posterior border of the sacral flange of the ilium (ligamentum sacro-iliacum dorsale longum, Schmaltz); (3) a broad sheet of ligament extending between the transverse lamina of the sacrum, obliquely downward and backward to the dorsal border of the ilium above the acetabulum (spina ischiadicum) and to the dorsal border of the ischium as far back as the ischial tuberosity (ligamentum sacro-spinosum et tuberosum, Schmaltz); (4) a number of oblique ligaments springing from the anterior dorsal edge of the sacral flange of the ilium and running to the spines of the lumbar vertebrae.

The ligaments above described are of great importance both in tying the pelvis securely in place and in

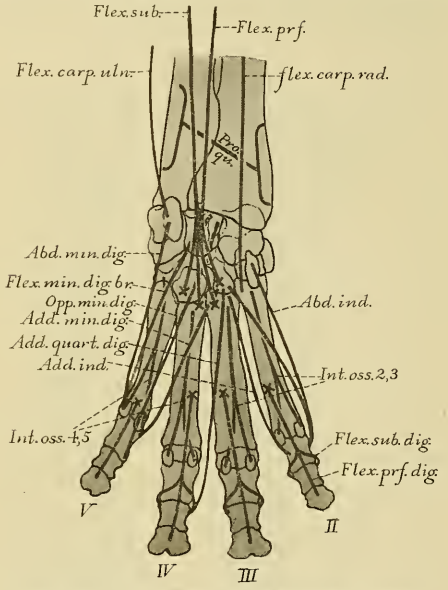


FIGURE 656.—Arrangement of the muscles of the flexor surface of the manus of *Mesatirhinus petersoni*

Restoration of muscles based chiefly on dissection of the forefoot of a tapir by Murie after the removal of the palmaris longus, lumbricales, and parts of the flexor tendons (cut at x). One-third natural size.

affording origin to several of the great muscles of the loins, croup, and buttocks, as follows: No. 4 (above) affords partial insertion to the longissimus dorsi; Nos. 1, 2, 3 conjointly afford origin for the gluteus medius, gluteus maximus, and "biceps 1" (femorococcygeus).

MUSCULAR ATTACHMENTS OF THE PELVIS

The pelvis of *Palaeosyops* is of the subgraviportal type in which the ilium spreads widely and has its superior border well rounded out rather than concave. In correlation with this adaptation the area for the gluteus medius on the dorsum of the ilium and that for the iliacus on the venter of the ilium are both

wide; it is also highly probable that the gluteus medius did not extend over the dorsal edge of the ilium as it does in cursorial animals and therefore was not inserted into the fascia of the longissimus dorsi (Gregory, 1912.1, p. 292). The superior border or crest of the ilium gave attachment to the superficial fibers of the longissimus dorsi and also to the obliquus abdominis externus and obliquus abdominis internus; the outer part of the superior border gave origin to the tensor fasciae femoris and to the inguinal ligament. The gluteus maximus may possibly have barely touched this border. The area for the gluteus minimus immediately above the acetabulum is roughened and streaked, probably indicating that the muscle was divided into a number of twisted and parallel strands as in *Equus*. Immediately in front of the acetabulum is a deep pit for the rectus femoris (the latter, according to Windle and Parsons, homologous with the reflected head of the rectus in man). On the neck of the ilium, on the antero-internal surface, is a pit for the psoas parvus; below this pit the sartorius probably took rise from the fascia of the ilio-psoas.

The antero-internal surface of the ilium (corresponding to the iliac fossa of man) lodges the wide iliacus; between the area for the iliacus and the pit for the psoas parvus is a gently depressed surface homologous with a similar region in the horse and likewise bearing a nutrient foramen (arteria circumflexa femoris lateralis, Schmaltz). Dorsomedial to the iliac fossa and below the articular surface for the sacrum the ilium exhibits a flattened elongate surface which as in the horse and tapir probably lodged an anterodorsal extension of the obturator internus.

The lower part of the pelvis (that is, the pubis, ischium, and acetabular borders) in a general way gives origin to two principal groups of locomotor muscles—to the abductors of the femur, which are inserted either in the digital (trochanteric) fossa or immediately below it, and to certain flexors of the femur—the ischial head of the biceps femoris ("biceps 2"), the semitendinosus, and the semimembranosus. Immediately behind the ischial spine and the area for the gluteus minimus the superior ramus of the ischium is smoothly rounded, this indicating the place where the obdurator internus came over the ridge on its way toward the femur. Immediately below this place, above and behind the acetabulum, is a small roughened area which probably indicates the position of the gemelli (Pl. XLIV).

The ventral border of the symphysis pubis probably gave origin to the closely interminglingadductor magnus and gracilis, while the lower borders of the thyroid (obturator) foramen, as well as parts of the symphysis, gave origin to the obturator externus.

Near the posterior end of the ischium and on or near the dorsal external border is a long, low prominence for the true biceps femoris (caput longum of *Homo*); this contrasts with that of *Equus*, which has grown outward and downward into a great horizontal flange (the crista tuberis ischii, Schmaltz). Although the bicipital prominence in *Palaeosyops* and the bicipital flange in *Equus* are so different in appearance that we do not at first recognize their homology with each other, yet they are clearly homologous, because the rhinoceroses *Hyrachyus* and *Caenopus*, *Eohippus* and other extinct perissodactyls, as well as *Tapirus*, afford intermediate conditions. Cuvier and Laurillard's plates also show that in many mammals the long head of the biceps femoris arises from the same region we have assigned to it in *Palaeosyops*. Immediately below the prominence for the biceps femoris is the probable location of the ischial head of the semitendinosus, while below and in front of the latter is the probable origin of the quadratus femoris. The region of the ischial tuberosity very probably served for the ischial head of the semimembranosus.

The anterior ramus of the pubis probably gave origin to the pectineus; on its anterior border there is little if any iliopectineal eminence, the latter being very prominent in *Tapirus* and *Equus* and serving in part for the origin of the pectineus (Schmaltz, 1909.1, Taf. 7, 51).

The obturator (thyroid) foramen on its inner side and around its border was probably filled by the obturator internus, which also sent forward and upward a branch lying above and medial to the area for the iliacus. By comparison with *Equus* and *Tapirus* it seems very probable that in *Palaeosyops* the obturator internus arose inside the true pelvis, as in the Perissodactyla generally as well as in the Hyracoidea and the Proboscidea, whereas in the Artiodactyla it arises outside the pelvis (Windle and Parsons).

MUSCULAR ATTACHMENTS OF THE FEMUR

The femur as a whole in *Palaeosyops* and still more in Oligocene titanotheres is much more elephantine than horselike. The shaft is flattened, the patellar trochlea faces more anteriorly, the limb is straighter at the knee. The long flattened subvertical femur of the graviportal elephant is inclosed in front and at the side by a long vastus externus, of great transverse diameter; the short round femur of *Equus* and of the kangaroo is covered by a balloon-shaped vastus externus of great anteroposterior diameter. The femur of *Palaeosyops* has the appearance of having been flattened by the pressure of the vastus externus in front and by the lateral strain of the great gluteus maximus along the outer side. The long and transversely wide vastus externus of the femur contributes to the great weight-lifting power and feeble jumping or saltatorial power of the limb; while the balloon-

shaped vastus of the horse and kangaroo contributes to the far greater saltatorial power.

On the front face of the femur the massive but low great trochanter gave attachment to the gluteus medius. The region between the great trochanter and the head is widened and exhibits laterally the upper limits of the area for the vastus externus; in the midline is a roughened line separating the area of the vastus externus from that of the vastus internus, as in *Tapirus*. The area for the vastus externus (which in *Tapirus* was probably a very large muscle covering the entire length of the shaft of the femur) is not visibly separated below from the area for the crureus, which probably covered the front and lower outer part of the shaft.

Outer edge of the femur: The great trochanter bears on its upper and external faces the area for the gluteus medius. The third trochanter bounds externally the area for the vastus externus and on its outer crest gives insertion to the deep slip of the gluteus maximus; the low ridge leading down from the third trochanter to the shaft may also have given insertion to fibers of the gluteus maximus.

About 3 inches above the ectocondyle is the ridge for the external head of the gastrocnemius. Immediately below the gastrocnemius ridge is the deep plantar fossa facing posteroexternally and giving origin to the tendon of the plantaris (flexor sublimis).

The external tuberosity of the femur (above the ectocondyle) bears on its outer face a deep pit for the collateral femorotibial ligament. Lying between the last-named pit and the patellar trochlea is the pit for the tendon of the extensor longus digitorum, while behind this in turn and above the condylar surface is a circular deep pit for the tendon of the popliteus. (Possibly also the femoral portion of the peroneus longus may have arisen here. Compare Windle and Parsons, 1901.1, p. 278.)

The posterior surface of the femur shows especially the following structures: (1) The great trochanter, bearing the posterior portion of the area for the gluteus medius; (2) the digital or trochanteric fossa, lodging the obturator internus, gemelli, and obturator externus; the quadratus femoris may have been inserted below these; (3) the second trochanter (trochanter minor), giving insertion both to the psoas and to the iliacus; (4) the third trochanter, for the gluteus maximus; (5) the area for the pectineus, lying toward the inner border and some distance below the second trochanter. A foramen for a branch of the femoral artery lies below the last-named area and in about the middle of the internal posterior edge of the femur. (6) The linea aspera (plainly shown in the femur, Am. Mus. 11690) lies in the middle third of the posterior face of the femur near the internal border and below the area for the pectineus; in this region bounded by the linea aspera internally and by the downward prolongation of the third trochanter the adductor longus was probably inserted.

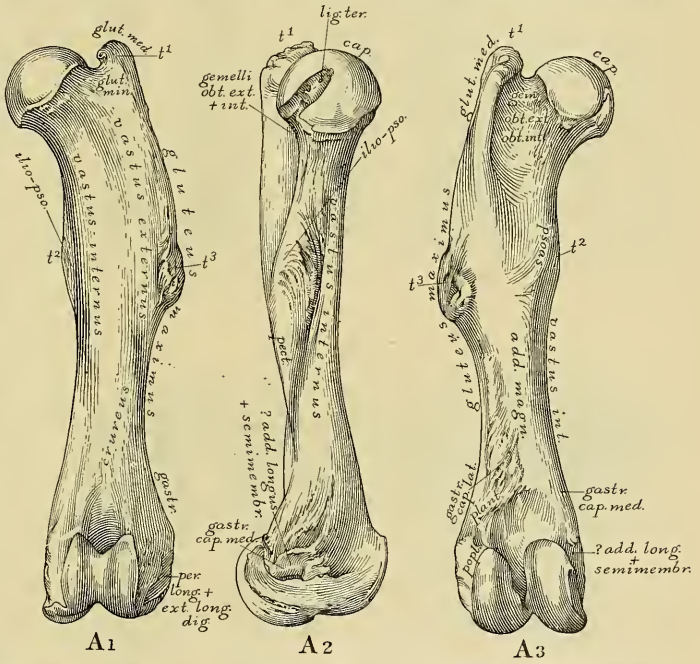


FIGURE 657.—Left femur of *Brontops robustus* (type), showing probable position and attachments of principal muscles

A_1, Front view; A_2, inner side view; A_3, back view. One-eighth natural size.

Inner face of the femur: The principal topographic features of the inner face of the femur are as follows: (1) The pit for the ligamentum teres; (2) the prominent second trochanter, roughened for the attachment of the iliacus and psoas; (3) the area for the vastus internus along the inner shaft; (4) the foramen for the femoral artery; (5) near the lower end the area for the internal head of the gastrocnemius; (6) above the internal condyle a vertical ridge for the adductor and semimembranosus; (7) below this the pit for the ligamentum collaterale laterale.

MUSCULAR ATTACHMENTS OF THE PATELLA

The more or less pear-shaped patella (morphologically the sesamoid of the quadriceps femoris) is on the whole more elephantine than horselike, in correlation with the straighter limb. It differs from that of *Tapirus* in having the dorsal prominence for the rectus sessile instead of hooklike; the upper surface is anteroposteriorly deep and flat; the lower end for the ligament of the patella is prolonged and pointed; the inner side is not produced. Correlated with the latter structure is the small size of the inner patellar keel on the femur, this keel not being globose above, as it is in *Equus* and to a less extent in *Tapirus*. All this implies that, unlike *Equus*, *Palaeosyops* could not rest the patella on top of the inner patellar keel of the femur but stood with straighter limb.

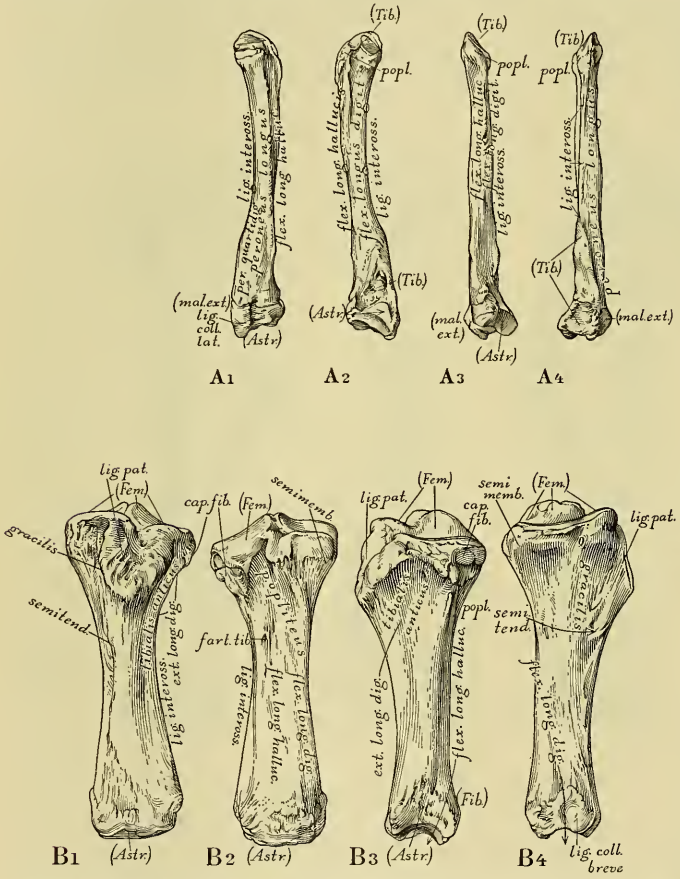


FIGURE 658.—Left fibula and left tibia of *Brontops robustus* (type), showing probable position and attachments of principal muscles

A1, Fibula, outer side; A2, inner side; A3, rear view; A4, front view. B1, Tibia, front view; B2, rear view; B3, outer side; B4, inner side. One-eighth natural size.

MUSCULAR ATTACHMENTS OF THE TIBIA

The tibia is rather similar to that of *Tapirus*. On the cnemial crest the surface for the ligamentum patellae (which was probably tripartite, as in the horse) faces more upward than in *Tapirus*, in correlation with the straighter limb, but is otherwise similar.

The cnemial crest is somewhat less reflected than it is in *Tapirus*. It terminates above in a supero-external tuberosity, which not only gave origin to a part of the ligamentum patellae but probably also gave insertion to some of the deeper strands of the biceps femoris (ischial head). Immediately postero-external to this bicipital tuberosity is a large, deep vertical groove for the tendon of the extensor longus digitorum. The tendon is attached to the femur immediately above the groove.

Immediately below the extensor groove and behind the cnemial crest is the fossa for the tibialis anticus, covering the inner face of the tibia but not defined below and nowhere as sharply defined as in *Tapirus*. The front of the cnemial crest served chiefly for the inferior prolongation of the ligamentum patellae, but the lower end of the crest bears a prominent scar, into which was inserted a deep strand of the semitendinosus which passed across the inner face of the tibia on its way to the fascia of the shank.

On the inner surface of the tibia, behind the cnemial crest, the area for the gracilis is not defined, but no doubt that muscle was inserted in this region. The inner tuberosity, a low prominence behind the middle line on the proximal border, together with the pit behind it, possibly gave insertion to a deep slip of the semimembranosus and also to the ligamentum collaterale tibiale.

Most of the inner or medial surface of the tibia was free of muscular attachments (planum subcutaneum, Schmaltz). Distally the inner face bears near the front border a sharply flattened prominence for the ligamentum collaterale breve running obliquely to the astragalus and calcaneum. Some distance behind this prominence is a vertical groove for the flexor longus digitorum. The back of the tibia below the popliteal notch is taken up by a wide and deep fossa for the popliteus. This muscle may also have extended around on to the inner surface of the tibia,

but only to a slight extent. The popliteus area is bounded below by the indistinct popliteal or oblique line, here indicated chiefly by a low prominence extending from the upper external edge obliquely downward and inward across the middle third of the back of the shaft. To this oblique line may very possibly have been attached remnants of the soleus (which in *Tapirus* has lost its sheathlike character), a muscle degenerated into an elastic band and shifted in origin upon the popliteal surface of the femur (Murie).

The lower third of the back of the shaft terminates below in a posterodistal process which in the standing pose of the horse juts down between the back of the astragalus and the sustentaculum of the calcaneum. Postero-externally to this process the flexor longus hallucis and probably the tibialis posticus passed downward.

The flexor longus hallucis and the flexor longus digitorum have been confused by certain authors. In man the flexor longus digitorum passes through the groove behind the internal malleolus of the tibia, while the flexor longus hallucis passes down behind the sustentaculum of the calcaneum (Cunningham, 1903.1, pp. 229, 236, 178, fig. 170), and the same is true of the horse (Schmaltz, 1909.1, Taf. 56, fig. 1); and yet Murie mistakenly calls the muscle which "glides in the groove behind the malleolus of the tibia" "flexor longus hallucis," while the tendon which lies "behind the os calcis" he calls "flexor longus digitorum," thus reversing the implied homologies with man, as very clearly shown in his figures. Even Windle and Parsons seem to be wrong, for they homologize with the flexor longus hallucis the muscle which "winds round the internal malleolus" (1903.1, p. 281). The flexor longus hallucis in the tapir joins the flexor longus digitorum, the latter forming the perforating tendons (flexor profundus) of the three digits. The tibialis posticus is not recognizable in the tapir (Murie, 1872.1, p. 166) nor in some artiodactyls and *Hyrax* (Windle and Parsons, 1903.1, p. 282), but is probably fused with the flexor longus hallucis. In the horse it is large and distinct (Schmaltz, 1909.1, Taf. 59, 53, 56). In the Sumatran rhinoceros it is fused with the flexor longus hallucis and flexor longus digitorum, these three together forming the flexor communis digitorum (Beddard, 1889.1, p. 22). In the elephant it is distinct. It seems not unlikely that in Eocene graviportal ungulates such as *Palaeosyops* the muscle was present and more or less appressed to the flexor longus hallucis. It may then have had an area on the back of the tibia just below the popliteal line and possibly another on the back of the fibula, behind the flexor longus hallucis.

The soleus is another muscle of somewhat doubtful form and attachments. In man this broad muscle lies beneath the gastrocnemius and is broadly attached to the back of the fibula and to the popliteal or oblique line of the tibia; it is inserted into the tendo Achillis and assists in lifting the heel. In many ungulates, however, the soleus is of small size (Windle and Parsons, 1903.1, p. 280) and more or less cordlike; it probably contributes by its elasticity to the quick backward jerk or kick of the foot. In the tapir the soleus is very small and cordlike; it has shifted its origin up to the femur, in the popliteal space, behind the gastrocnemius area, and is here closely associated with the cordlike tendinous plantaris (Murie, 1872.1, p. 163 and pl. 10, fig. 13). In this extreme modification of the soleus the tapir is more specialized than either the horse, in which a slender belly of the soleus remains attached to the tibia behind the head of the fibula, or the rhinoceros, in which as figured by Beddard (1889.1, p. 21) the soleus is fleshy and apparently arises below the popliteus. In the elephant the soleus is well developed. It therefore seems likely that *Palaeosyops* and the Oligocene titanotheres avoided the extreme degeneration of the soleus which is characteristic of the tapir and retained a fleshy soleus, attached to the oblique or popliteal line of the tibia and possibly to the back of the upper part of the fibula.

MUSCULAR ATTACHMENT OF THE FIBULA

As compared with that of *Tapirus* the fibula of *Palaeosyops* has both proximal and distal ends larger and not so flat; the middle of the shaft is flatter. To the outer side of the head of the fibula was attached the peroneus longus, which extended down the front outer face of the shaft and passed to the foot through a deep peroneal groove. The top of the fibula (caput fibulae) behind the surface for articulation with the tibia shows an expanded smooth prominence, posterointernal to which was a groove; over both prominence and groove slid the tendon of the popliteus. Below the popliteal prominence the flexor longus hallucis probably took up most of the posterior surface of the shaft. The inner or medial face of the fibula was also largely filled by the flexor longus hallucis. The front apex of the external malleolus was probably attached to the "ligamentum collaterale longum" running to the calcaneum.

MUSCULAR ATTACHMENTS OF THE PES

The distal rugosity of the tuber calcis served as the insertion area for the following tendons: (1) The true tendo Achillis, which consists of the paired tendons of the gastrocnemius; (2) the complex of tendinous sheaths which descend from the biceps, gracilis, and semitendinosus and enwrap the tendon of the gastrocnemius; (3) the tendon of the plantaris. This tendon

arises beneath the gastrocnemius, but lower down near the heel it comes to the surface, curves around the tendon of the gastrocnemius, then out, "spreading over the surface of the os calcis, partly attached to either side it continues into the sole of the foot." (Murie, 1872.1, p. 163.)

The back of the tuber calcis is roughened for the "ligamentum tarsi plantare longum" (Schmaltz,) which was inserted into the large tuberosity on the back of the cuboid.

The sustentaculum calcanei on its posterior surface bears a long vertical groove, lying next the shaft of the calcaneum; this groove lodged the tendon of the flexor longus hallucis. The medial tip of the sustentaculum is roughened for the ligamentum tarsi tibiale breve, which passed across to a superior postero-internal process on the astragalus.

On the front face of the calcaneum the coracoid process (above the ectal facet) bears on its superior face two deep pits; the inner and larger one receives the

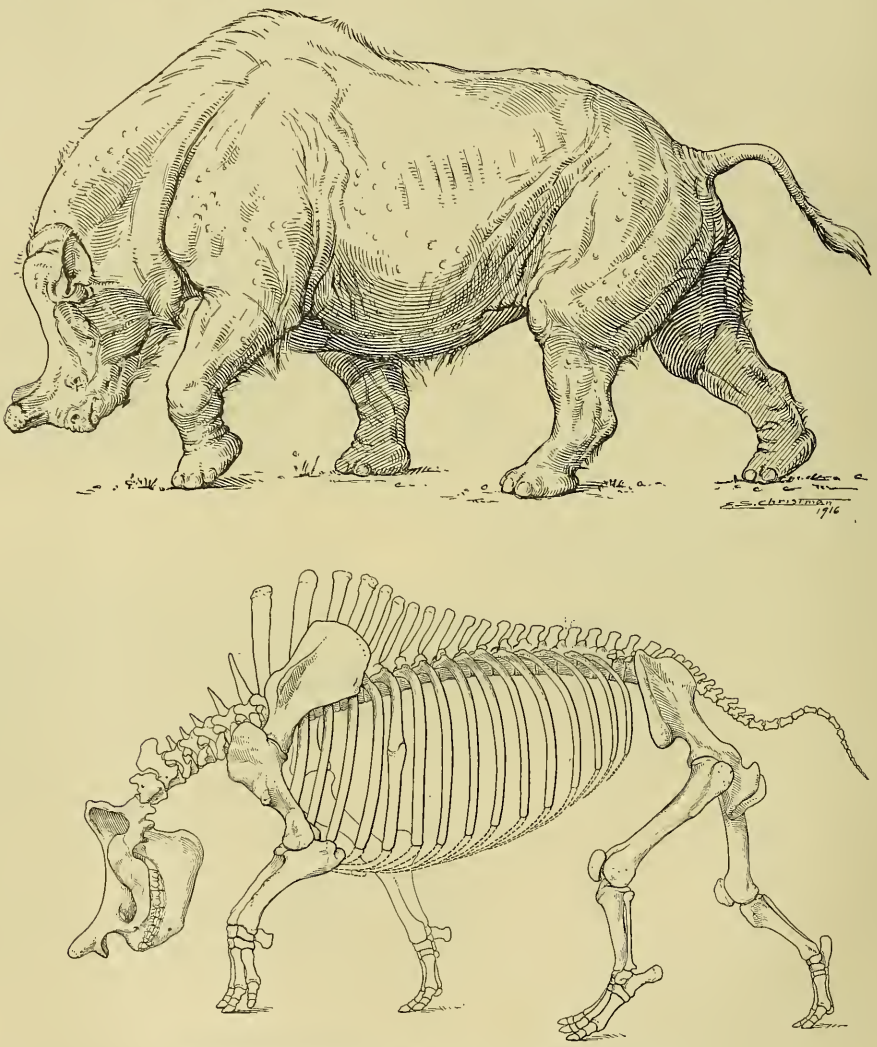


FIGURE 659.—Skeleton and restoration of *Brontops* cf. *B. robustus*

Based on the mounted skeleton in the American Museum of Natural History and on the studies summarized in the text. One twenty-fifth natural size.

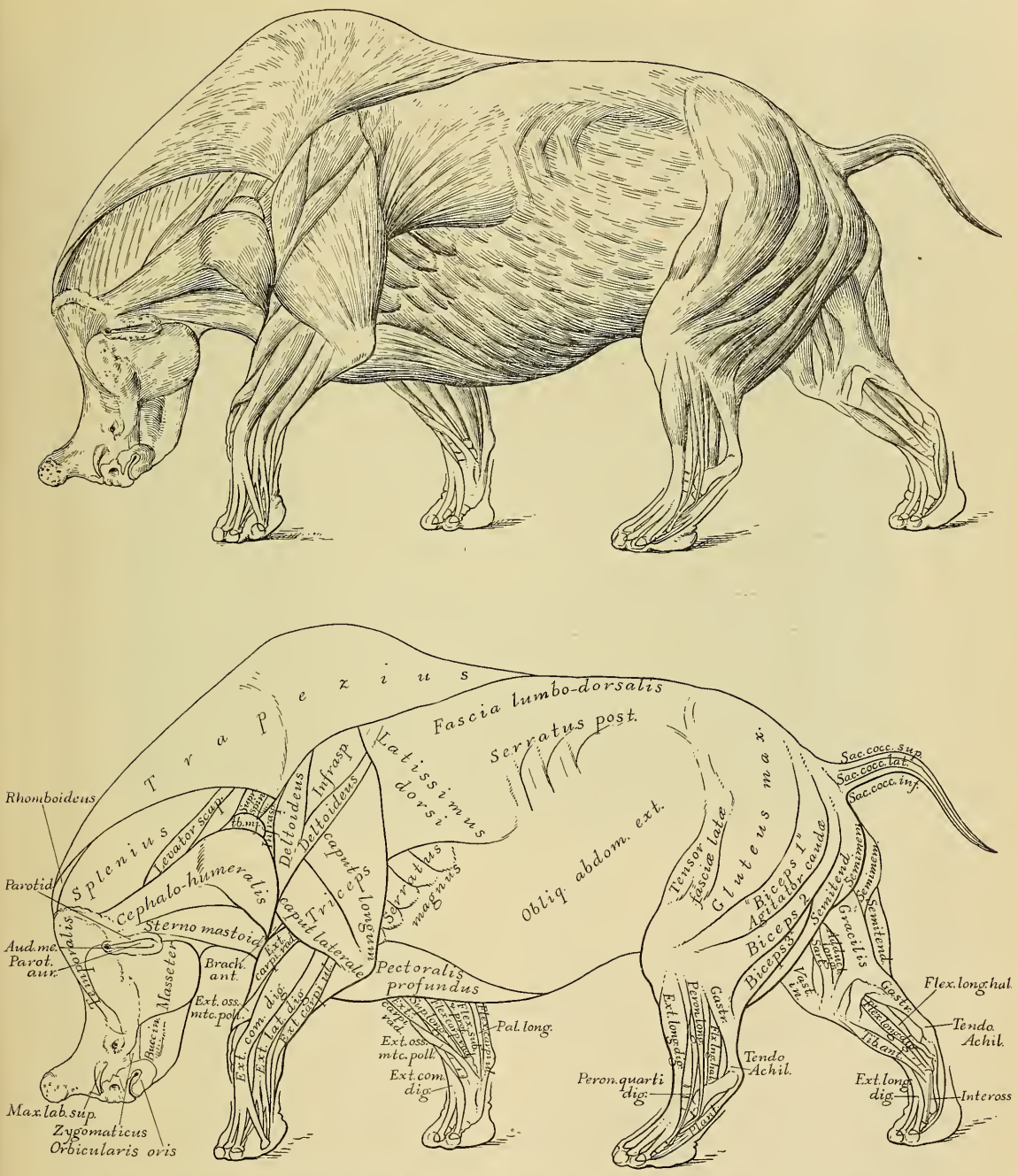


FIGURE 660.—Restoration of the superficial muscles of the body of an Oligocene titanothere (*Brontops* cf. *B. robustus*) after the removal of the panniculus

Drawn by Erwin S. Christman. About one twenty-fifth natural size.

posterior tip of the fibula in extreme flexion of the foot; the outer smaller pit is for the "ligamentum tarsi fibulare breve" (Schmaltz), which passes to the outer side of the calcaneum. The lower fourth of the shaft of the calcaneum above the cuboid facet is externally roughened, apparently for the "ligamentum tarsi fibulare longum" and perhaps also for the extensor brevis digitorum. The external keel of the astragalar trochlea bears externally an articular band for the fibula. Partly surrounded by this band and lying behind it is a deep pit for the "ligamentum tarsi fibulare breve."

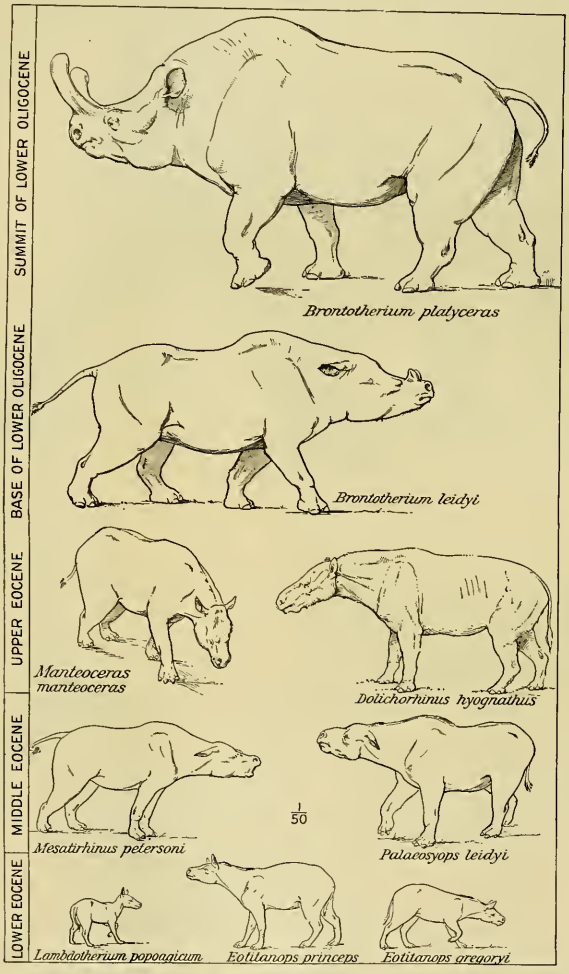


FIGURE 661.—Restorations of nine species of titanotheres from the lower, middle, and upper Eocene and lower Oligocene

Drawn by Mrs. E. M. Fulda. About one-fiftieth natural size

On the inner side of the astragalus the posterosuperior corner bears a large process for the "ligamentum tarsi fibulare breve." The same ligament was probably continued into the pit which lies below and in front of the last-named process. Also on the inner side of the astragalus near the lower end, above the navicular facet, is a high prominence, apparently for the ligamentum tarsi tibiale longum. Immediately above this prominence passed the tendon of the tibialis on its way to insertion on the proximal end of the second metatarsal.

The roughened anterior faces of the navicular, cuneiforms, and cuboid doubtless betoken the ligaments connecting these bones with the astragalus and tibia. The roughened protuberance on the back of the cuboid served not only for the insertion of the ligamentum tarsi plantare longum as stated above but also for the origin of the interossei muscles on the sole. The large prominence on the back of the entocuneiform gave origin to the first interosseus. The front faces of the three metatarsals were probably overlain by the several bellies of the extensor brevis digitorum, which in the tapir passes down from the front of the calcaneum, from the ankle ligament and bones beneath, to the proximal phalanx of the middle toe, lateral slips being given off to the proximal phalanges of digits II and IV.

The proximal end of Mts II is roughened on its medial face for the tendon of the tibialis anticus and probably for the "ligamentum tarsi tibiale longum." The outer surface of Mts IV is roughened near the proximal end, probably for a branch of the plantaris ligament.

The shafts of the metatarsals on each side in the proximal third are roughened for the interossei and adductors, which as in *Tapirus* may have consisted of three pairs. (Murie, 1872.1, p. 166.)

The sides of the proximal phalanges, as in the manus, are roughened proximally for the interossei and probably to the lumbricales. The laterodistal pits are for collateral ligaments, the dorsal face, proximal end, for the extensor brevis digitorum. On the plantar side the proximal phalanges were overlain by the perforated tendons of the plantaris, which were inserted into the sides of the second phalanges.

In the ungual phalanges the dorsal face, proximal portion, gave insertion to the extensor longus digitorum; the plantar face gave insertion to the flexor communis digitorum (flexor perforans).

The lumbricales, which in *Tapirus* are very fully developed, were attached to the sides of the flexor tendons and were inserted on the proximal sides of the first row of phalanges.

SECTION 5. MUSCLES OF THE LIMBS AND VERTEBRAE OF OLIGOCENE TITANOTHERES

The more robust development and marked broadening of many of the limb bones of the Oligocene titanotheres as compared with those of the Eocene titanotheres indicate corresponding changes in the muscles. The principal attachments of the limb muscles are indicated in Figures 652–660.

SECTION 6. RESTORATION OF THE MUSCULATURE AND BODY FORM OF BRONTOPS ROBUSTUS, AN OLIGOCENE TITANOTHERE

The restoration of *Brontops robustus* is based, first, upon a detailed study of the musculature of each bony element of the skeleton, as described above, and second, upon a comparative study of the general appearance of the musculature of the body as a whole in recent perissodactyls, as figured by several authors. Some valuable hints were obtained from photographs of partly dissected specimens of the white rhinoceros, taken in the field by Herbert Lang, and from figures of the Indian elephant by Cuvier and Laurillard.

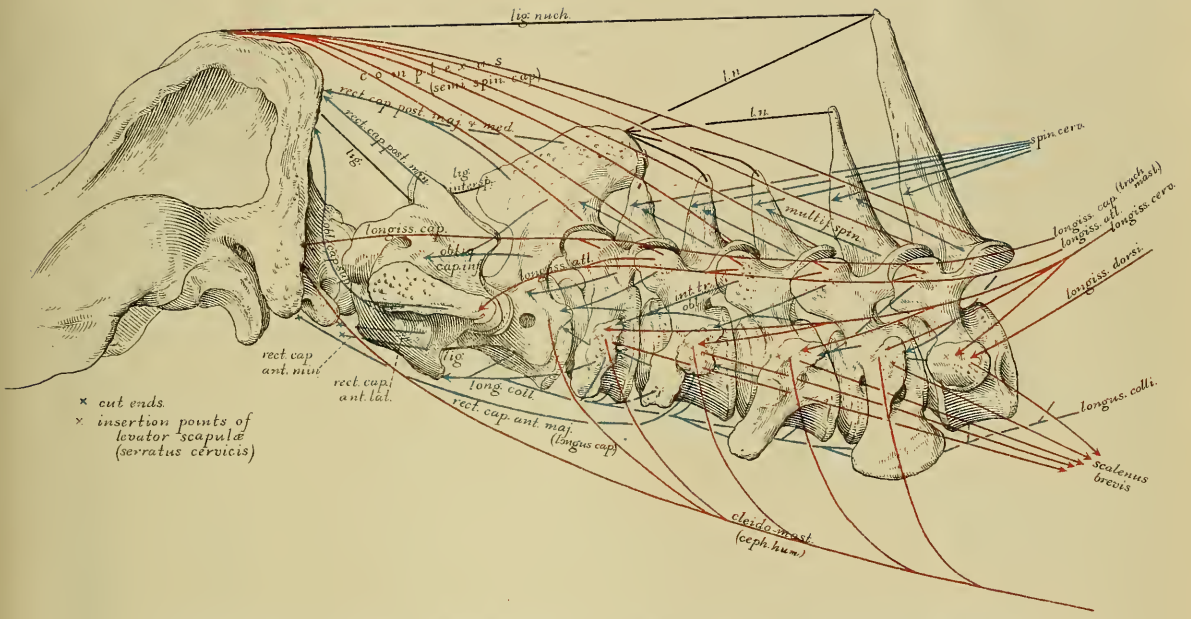
The first step toward insuring a lifelike pose in the restoration of the living animal was to obtain a correct pose for the skeleton. A cardboard manikin based upon the mounted skeleton in the American Museum was drawn to scale; in this manikin each movable element of the skeleton was fastened to flexible copper wire, so that the pose could be readily changed. The pose finally adopted represents the animal in rapid forward motion with the head lowered, as if for attack. The position assigned to the limbs is that commonly assumed under such conditions by graviportal types, such as the elephant and rhinoceros. The scapula is placed well above the ribs, as in ungulates generally, and not so far down as it is in the mounted skeletons of titanotheres in the museums. When placed in this pose the fore part of the skull is still some distance above the ground. In order to lower the mouth to the ground the animal possibly extended one fore limb far forward and the opposite fore limb backward.

After the skeleton was drawn in this pose (fig. 659) an outline tracing of this drawing was used as a basis for the placing of the muscles. There can be little doubt as to the general position of the chief muscles as seen after the removal of the panniculus and platysma layer; but the precise form and size of each muscle are of course more or less doubtful. In every case, however, we are guided, so far as possible, by the conditions observable in recent perissodactyls and to some extent in the elephant.

In the life restoration the skin is of the pachyderm type, intermediate in character between those of elephants and rhinoceroses but somewhat more hairy. Possibly the color was more or less uniformly dark gray. The feet are intermediate in character between those of the rhinoceros and the elephant, as shown by the skeleton.

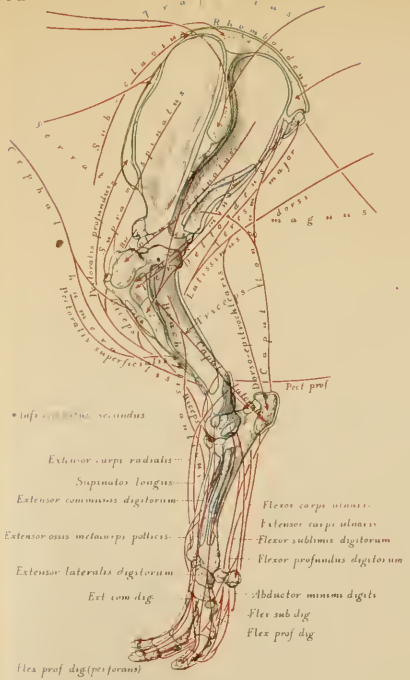
FIGURE 662.—Restoration of *Brontotherium gigas*

Modeled by E. S. Christman under the direction of W. K. Gregory. Based on the studies of the musculature and skeleton described in Chapter VIII. The relative length of the skull and forearm and the depth of the thorax at the shoulder were determined from Am. Mus. 492. About one thirty-second natural size.



PROBABLE ARRANGEMENT OF THE MUSCLES OF THE OCCIPUT AND NECK IN AN OLIGOCENE TITANOTHERE (BRONTOPS ROBUSTUS) AFTER THE PLATYSMA, SPLENIUS, RHOMBOIDEUS, TRAPEZIUS, AND LEVATOR SCAPULAE HAVE BEEN REMOVED

One-sixth natural size. Blue lines indicate deep muscles, red lines superficial muscles, and black lines the ligamentum nuchae; x (blue) indicates a cut end of a muscle, and x (red) the origins of slips of the serratus cervicis (levator scapulae). To the uttermost rim of the lambdoidal crest was attached the splenius, and below this, on the back of the mastoid region and paroccipital process, were the longissimus capitis and cephalo-humeralis (cleido-mastoid). Beneath the splenius was the complexus (semispinalis capitis). The nuchal surface of the occiput was filled by the obliquus capitis superior, the rectus capitis posticus major and minor, and the ligamentum nuchae. (*After Gregory and Christman.*)



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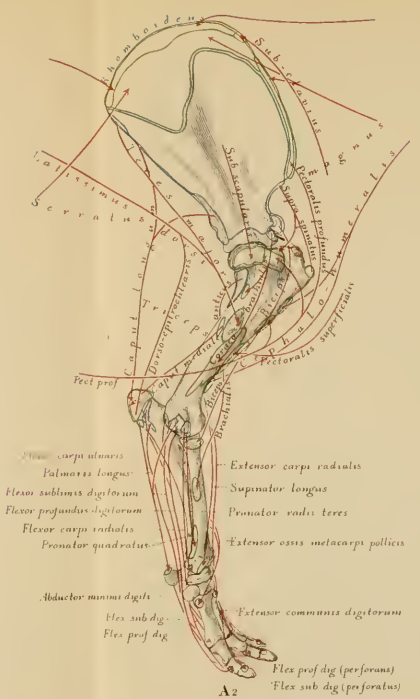

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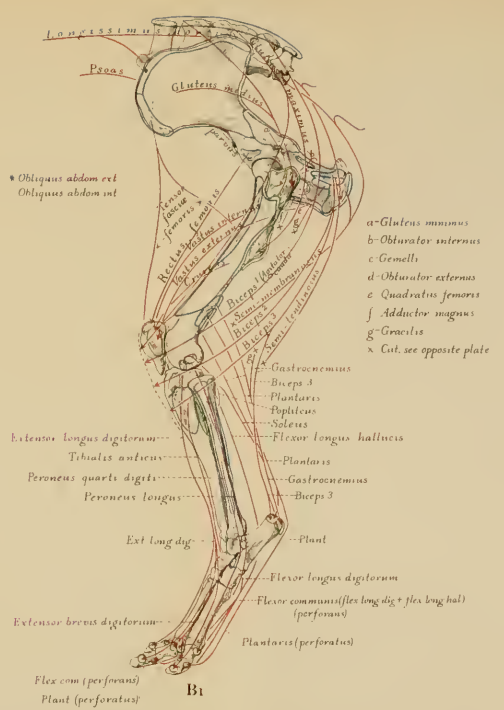
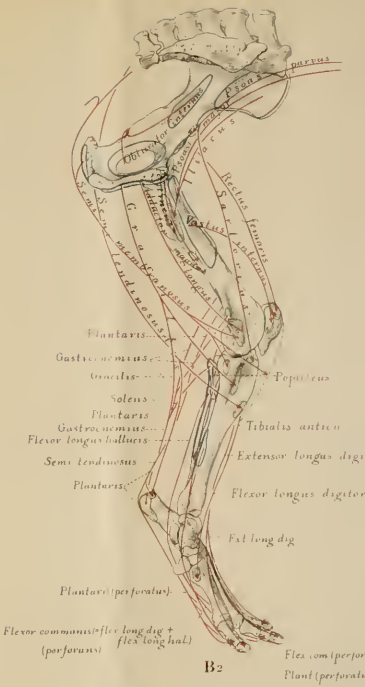


B1



B2

MUSCULATURE OF THE FORE AND HIND LIMBS OF PALAEOSYOPS LEIDYI

This shows the probable origins (blue), insertions (green), and general courses (red) of the principal muscles. A1, Left fore limb, outer side view. A2, The same, inner side view. B1, Left hind limb, outer side view. B2, The same, inner side view. (*After Gregory and Christman.*)

CHAPTER IX

MECHANICS OF LOCOMOTION IN THE EVOLUTION OF LIMB STRUCTURE AS BEARING ON THE FORM AND HABITS OF THE TITANOTHERES AND THE RELATED ODD-TOED UNGULATES

The facts presented in this chapter should be studied in connection with those given in Chapter VIII on musculature and bone structure. Together these sections afford a complete interpretation of the mechanical evolution of the titanotheres.

SECTION I. ADAPTATION TO LOCOMOTION IN THE LIMBS OF THE FLEET (CURSORIAL) AND THE PONDEROUS (GRAVIPORTAL) TYPES OF TITANOTHERES AND OTHER HOOFED QUADRUPEDS

MECHANICAL AND PHYSIOLOGICAL PRINCIPLES GOVERNING THE PROPORTIONS AND ANGULATION OF LIMB SEGMENTS IN GRAVIPORTAL UNGULATES

RESEARCHES MADE AND PRINCIPLES ESTABLISHED

The laws of limb adaptation here presented are the result partly of joint and partly of independent researches made for this monograph. In 1900 Osborn (1900.181) independently established the relations of the articular facets and joints to speed and weight, and in 1911 he planned a comparative measurement and investigation of the limbs and arches in the nine families of perissodactyls and other ungulates. Osborn and Gregory jointly established the laws of limb proportion in adaptation to speed and weight, respectively, which were in part published in advance by Gregory (1912.1). Gregory (1912) independently investigated and applied the mechanics of muscular limb action and leverages in relation to speed and weight. The text of this chapter has been jointly prepared by Osborn and Gregory.

The principle that the limbs of quadrupeds are compound levers and that the relative lengths of the upper, middle, and lower segments are adapted to specific muscular powers, loads, and speeds is applied in the present monograph to the elucidation of the adaptive contrasts between cursorial and graviportal ungulates.

The limb movements of living animals have been investigated by Borelli (1680.1), Marey (1874.1), Stillman (1882.1), Haycraft (1900.1), Luciani (1905.1), Muybridge (1907.1). From the evolutionary point of view there are the studies of Cope (1889.3), Osborn (1890.51; 1895.99, 1900.181), Gaudry (1906.1), Gregory (1912.1). Cope made some suggestions as to the relative length of limb segments in saltatorial, cursorial, and graviportal types. Osborn especially developed the subject of angulation of the limbs in relation to great weight and to the articular planes of the proximal and distal limb facets. Gaudry pointed out the limb convergence between such straight-limbed, ponderous ungulates as *Elephas*, *Uintatherium*, and *Pyrotherium* as well as the convergence between numerous cursorial animals (*Equus*, *Theosodon*). Matthew (1909.1, pp. 429–432) discussed the ratios of the limb segments in various carnivores and ungulates, in adaptation to cursorial and "rectigrade" modes of locomotion. Rütimeyer and Allen (1876) discussed the relative lengths of the different segments of the fore and hind limbs in the extinct and living species of the bison and introduced the ratio method for taxonomic purposes. This method was effectively used by Gidley (1903.1) in comparing the different genera and species of Equidae. A review of the mechanical principles of quadrupedal locomotion with special reference to the limbs of ungulates is given by Gregory (1912.1, pp. 268–269). The chief works are cited in the bibliography for this chapter.

PRINCIPLES OF LEVERAGE AND MUSCULAR ACTION

By William K. Gregory

The meaning of contrasting limb proportions and angulation in cursorial and graviportal animals becomes clear if we keep in mind the underlying mechanical and physiological facts and principles.

Observation and photographs of animals in motion at once reveal the simple fact that the limbs by suddenly straightening out and opening the angles at the joints raise the whole body and not only enable it to fall forward but alternately accelerate and check the action of gravity. An animal running on a treadmill reveals the almost equally important fact that the limbs when extended anteriorly tend to drag the ground backward and to pull the body forward. A standing horse might give the impression that the fore limbs were relatively passive props and that the hind limbs were the chief propellers, but a consideration of the action of the massive muscles of the fore limbs and study of a horse running on a treadmill show that the fore limbs also exert great strength in dragging the body forward, in raising the fore part of the body, and even in pushing it forward when the fore limb is extended backward. In most ungulates the fore limbs sustain the greater loads.

When the limbs are moving quickly they seem to swing with the regularity of a pendulum, and it has often been noted that in cursorial animals the limb muscles are bunched or concentrated toward the proximal or upper end of the limb, the muscles being pro-

longed distally as slender tendons; in this way the center of gravity of the limb is comparatively high and we get the rapid oscillation of a pendulum in which the bob or weight is placed near the pivot.

In graviportal animals, on the contrary, the limb muscles are more evenly distributed down the limb and the slender tendinous portions are shorter, so that we have the slower oscillation of a pendulum in which the weight is moved down the shaft. But the free swing of the limbs is alternately accelerated and retarded by the actions of the muscles, and the fore-and-aft movement is complicated by twisting, abduction, and adduction of the various segments of the limb.

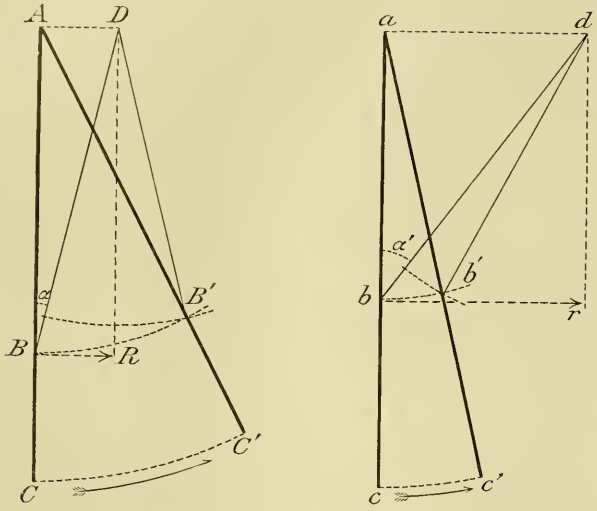


FIGURE 663.—Angles of muscular insertion and "parallelogram of forces." After Gregory, 1912.1

If the muscles contract at equal rates and the angle of insertion is acute (*ABD*) the extremity of a bone is moved through a wide arc (*CC′*), with feeble propulsive power (*BR*) and great lifting power (*AB*). As the angle of insertion increases (*abd*) the extremity of the bone is moved through a smaller arc (*cc′*) with greater propulsive power (*br*) and reduced lifting power (*ab*). If the muscles contract at unequal rates a slowly contracting muscle (*BD*) inserted at a small angle may move the insertion point slowly over a wide arc (*BB′*), whereas a more rapidly contracting muscle (*bd*) may move the insertion point more quickly but through a smaller arc (*bb′*).

When isolated for laboratory experiments, muscles react if stimulated according to relatively simple mechanical and physiological laws. An isolated muscle will contract upon stimulation to a varying fraction of its own length, from one-fifth to one-third. The force of a muscle—that is, its ability to overcome inertia at a given instant—is proportional to the number of muscle fibers cut in a cross section of the muscle; but the work that a muscle can perform during the entire period of its contraction is proportional both to the area of the cross section and to the length of the muscle—that is, the total work performed is proportional to the mass of the muscle; it is also inversely proportioned to the amount of inert connective tissue that is interspersed with the striped muscle fibers. Muscles when stretched serve as ligaments and help to prevent dislocation of the joints, as well as to transmit the pull of other muscles. Thus the biceps muscle and tendon assist in preventing dislocation of the shoulder; the quadriceps femoris and its tendons prevent dislocation of the knee joint; the serratus and its allies help to sling the body between the shoulders.

In general, long and slender muscles, such as the sartorius, exert a small force over a long range, while short and thick muscles, such as the gluteal mass in many ungulates, exert a great force through a short range. When the muscle fibers are set obliquely to the long axis of the muscle, as in the gastrocnemius, the muscle contracts slowly but with increased power. The contractile force is highest when a muscle is stretched to its full "physiological length" (that is, the greatest length it ever assumes during life), and the greatest force and velocity of contraction are developed when the movement of the muscle is checked during the initial stages and when the resistance is suddenly diminished. These principles operate constantly in the limbs, especially in the straightening of the knee joint, and in many cases where there is a sudden snap or jerk, as in the action of the flexors of the digits in a running horse.

It is a familiar dictum of elementary mechanics that in considering the action of levers "what is gained in speed is lost in power, and what is gained in power is lost in speed." In the skeleton these reciprocal relations of "power" and "speed" are affected not only by the relative distances between the fulcrum (joint), the force (of the muscle), and the load or resistance, but also by the "angle of insertion" of the muscle. If a man pulls a heavy door directly toward him (at right angles to the door) he will naturally find that it will move much more easily than when he pulls it at an oblique angle; but in the second case, although the effort required is greater, the movement of the door is much faster. The "angle of insertion" of a muscle is formed by the long axis of the muscle, its point of insertion, and the line between the insertion point and the fulcrum or joint. (See fig. 664.) If the angle of insertion is large, as in the gastrocnemius of graviportal animals, great power is secured. If the angle of insertion is small, as in the flexors and extensors of the digits, the movement of the insertion point may be very rapid.

From the diagram above referred to we learn that if two muscles contract at the same rate the lesser the

angle of insertion the greater will be the distance traversed by the insertion point in one second of time. From this it follows that if muscles contract at different rates the angles of insertion may be so adjusted as to keep constant the distance traversed in one second by the insertion point. The angle of insertion and consequently the reciprocal relations of speed and power change as the muscle contracts. In the case of the gastrocnemius the angle of insertion decreases as the heel is raised from the ground; in the case of the flexors of the digits the angle of insertion and consequently the "power" increases and the speed decreases as the muscles contract.

These variable relations of the rate of contraction, of the angle of insertion, and of the speed of the insertion points enable us in some measure to conceive the cooperative action of many muscles of varying lengths, speeds, and insertion angles, which may all be inserted at different points on a single bone and yet complete one cycle of movement in nearly the same time. It is also clear that in some muscles, as in the flexors of the digits, great speed may be developed at the beginning of a movement and great power with slow speed at the end, and vice versa.

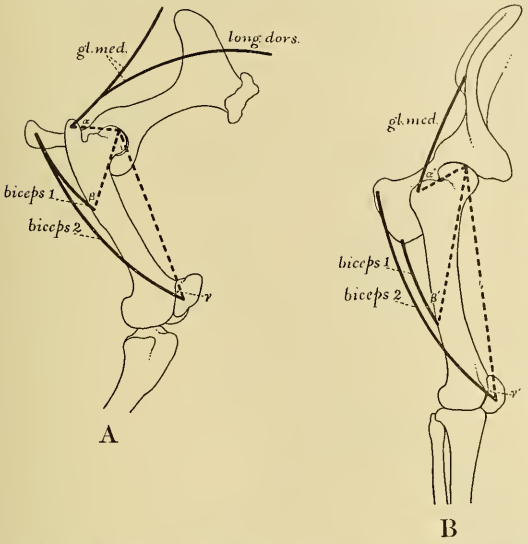


FIGURE 664.—Angles of insertion of certain extensor muscles to the pelvis and femur in the standing pose of a typically cursorial form (A, the horse) with relatively wide angles of insertion (α, β, γ) and in a typically graviportal form (B, the mastodon) with narrow angles of insertion (α', β', γ'). After Gregory, 1912.1

The heavy black lines represent the general direction of the muscles. The broken lines represent the radii of movement of the insertion points. In B the angle α' is probably too small—W. K. G.

Certain of the limb muscles (such as the coracobrachialis) are wrapped around spirally warped surfaces, and many of the joints between the segments (notably the astragalotibial joint) form segments of spirals, so that the mechanical advantages of the spiral wedge, or screw, are secured. By the proper regulation of the pitch of the screw either great "power" or great "speed" can be attained. For example, in extreme graviportal types the upper articular surface of the astragalus is very gently inclined downward and forward, corresponding to a wedge or screw of low pitch. In this way the very heavy load, represented by the pressure of the tibia upon the astragalus, is easily pushed up the gently sloping articular surface. In cursorial types, on the other hand, the upper articular surface of the astragalus faces more directly forward, and the pitch of the screw is relatively high. Under these conditions a relatively great expenditure of muscular energy is required, but the movement of the tibia upon the astragalus is correspondingly rapid.

The entire complex of the skeleton, of the musculature, and of the organs for developing and directing locomotive energy is adapted in cursorial animals for leaping and fast running, in graviportal animals for the evenly maintained forward sweep of the walk and amble. The elongate feet and bent limbs of cursorial forms when suddenly straightened out act more or less after the manner of a catapult in hurling the relatively light body forward. The very short feet and straight limbs of graviportal forms act as long-armed levers and low-pitched screws, which slowly

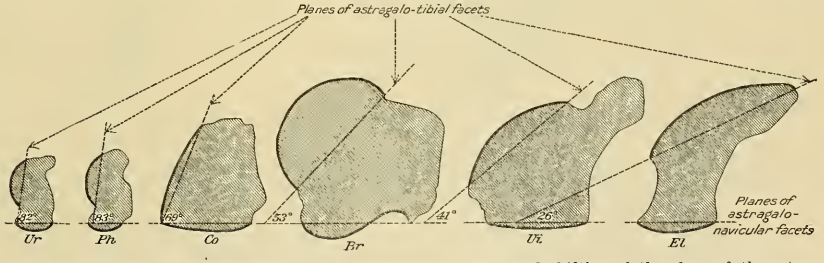


FIGURE 665.—Graviportal adaptation in the astragalus. Backward shifting of the plane of the astragalotibial facet from an angle of 82° in *Ursus* to an angle of 26° in *Elephas*, the plane of the astragalonavicular facet being taken as horizontal. After Osborn, 1900.148

Ur, Ursus; Ph, Phenacodus; Co, Coryphodon; Br, Brontops; Ui, Uintatherium; El, Elephas.

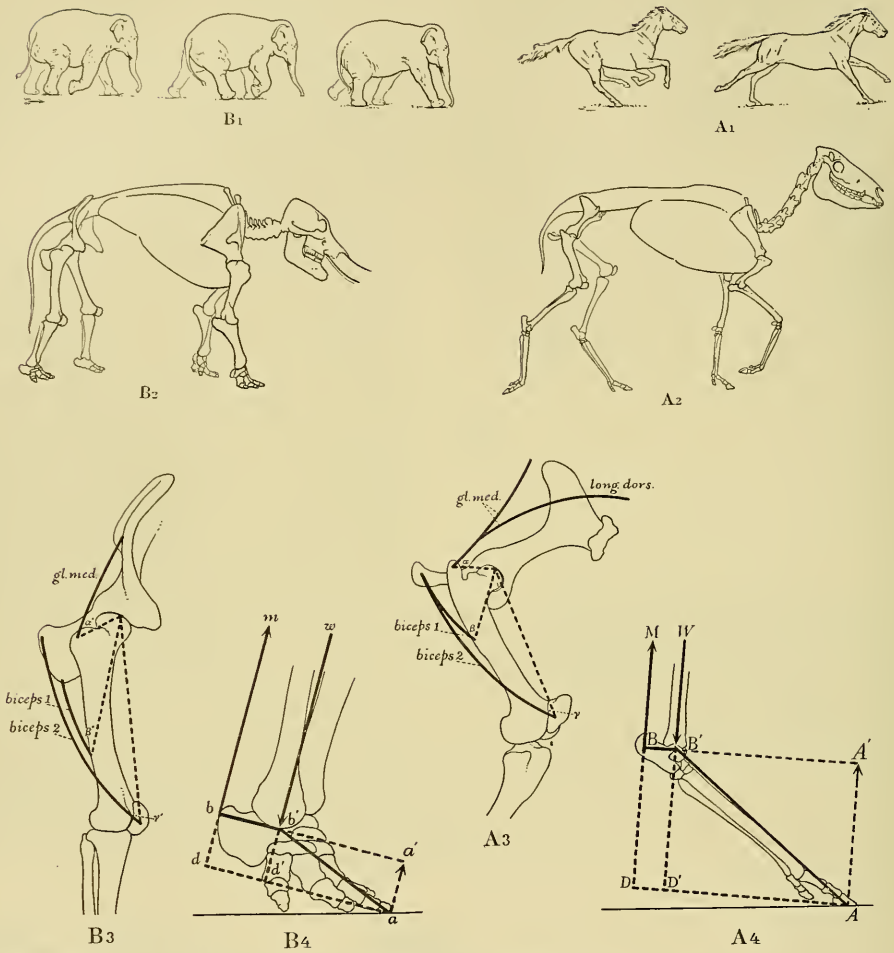


FIGURE 666.—Cursorial adaptation for the trot, run, and gallop in the horse (A_1–A_4); graviportal adaptation for the walk and amble in the elephant (B_1–B_4). After Gregory, 1912.1

A_1, The gallop of a horse, showing the leaping, catapult action of the slender limbs in a cursorial type.

B_1, The amble of an elephant, showing the steady sweep and great weight-lifting power of the ponderous limbs in a graviportal type.

A_2, B_2, Extremes of cursorial adaptation in a Miocene horse, *Hipparion* (*Neohipparion*) (A_2), and of graviportal adaptation in a mastodon (B_2).

A_3, B_3, Angulation of limb segments and muscles in a horse (A_3) and a mastodon (B_3):

Cursorial (A_3)	Graviportal (B_3)
Ilium and femur ar right angles in the standing pose.	Ilium and femur more nearly vertical.
Muscles inserted at open angles, giving great propulsive power.	Muscles inserted at more acute angles, giving great vertical or weight-lifting power.
Head of femur low, at right angles to shaft.	Head of femur high, at top of shaft.
Longissimus dorsi works in tandem with gluteus medius.	Longissimus dorsi cut off from gluteus medius.

A_4, Cursorial hind foot (*Hipparion*, *Neohipparion*), for springing and rapid lifting. B_4, Graviportal hind foot (*Mastodon*), for powerful, slow lifting. Fulcrum at B′, *b*′; power at B, *b*; resistance at A, *a*. If the pull of the calf muscles (M,m) and the weight at the ankle joints (W,w) were respectively equal, the long, cursorial foot would have great "moment of resistance" (W×B′A) and small "moment of power" (M×BB′), with high speed; whereas the short, graviportal foot would have relatively small moment of resistance ($w \times ba$) and great moment of power ($m \times bb'$), with slow speed.

lift, push, and pull forward the ponderous body. In more technical terms, the straightness of the limbs in graviportal animals is believed to have been evolved pari passu with the short rectigrade feet and with an ambling gait, while the bent or angulate

ascertaining the position and angulation of the limbs in extinct quadrupeds. The term angulation refers especially to the angles which exist between the main proximal and distal segments of the fore and hind limbs, namely, between the humerus and ulnoradius

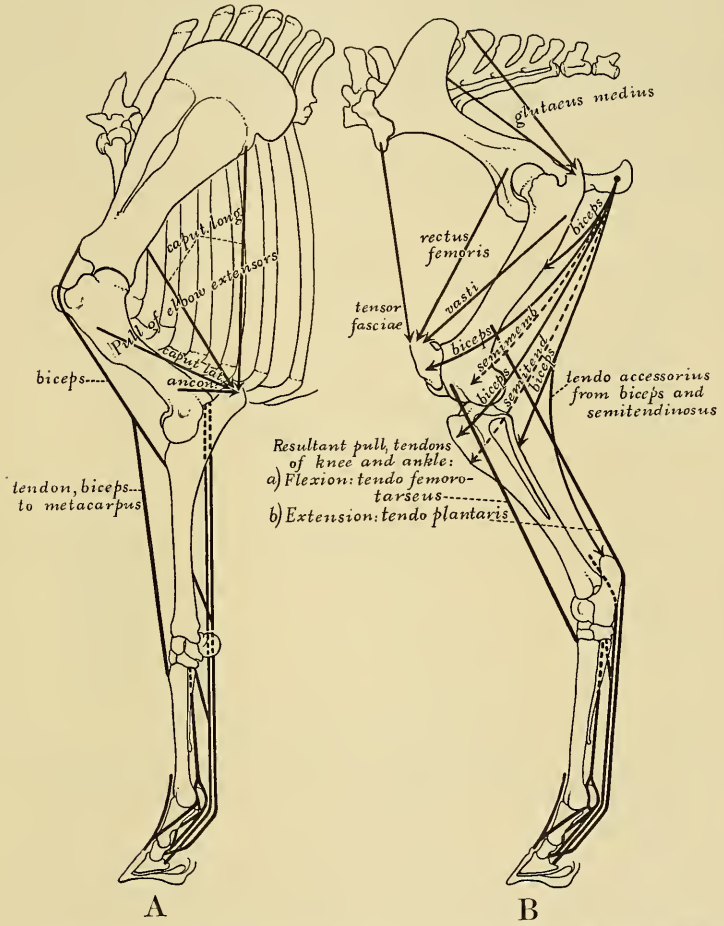


FIGURE 667.—Cursorial adaptation in the fore limb (A) and hind limb (B) of the horse

Upper segments short, angulate, with muscle insertions at open angles (power); lower segments elongate, muscle insertions oblique (speed). In the standing pose the opposing flexors and extensors are stretched through the weight of the animal and act more or less passively as ligaments. The equilibrium is maintained also by means of special tendons on opposite sides of the limbs. After Gregory (1912.1); adapted from Schmaltz (1905.1).

character of the limbs in cursorial animals is correlated with the very long, slender unguligrade feet and with a rapid running, bounding, galloping, or trotting gait.

STRAIGHTENING OF THE LIMBS AND ARCHES IN ADAPTATION TO GREAT WEIGHT (GRAVIPORTAL TYPE)

Angulation.—The author (Osborn, 1900.181), was led some years ago to study the various means of

and between the femur and tibiofibula. All primitive ambulatory and subcursorial ungulates exhibit sharp angles at the elbow and at the knee which are inherited from the unguiculate ancestors of ungulates. This acute angle is retained in all the cursorial and mediportal ungulates, but it tends to open out as the limbs become more vertical in the graviportal digitigrades and graviportal rectigrades.

From this we deduce the following law, which was partly formulated by the author in 1900 (op. cit., p. 94): The straightening of the ungulate limb is a secondary adaptation designed to transmit the increasing weight through a vertical shaft and thus relieve the muscles and ligaments from strain. Correlated with the straightening of the limb are the shifting of the proximal and distal articular facets of the humerus and of the femur into direct lines of pressure, and the alteration of the sections of the articular surfaces from an oblique to a right angle, or a horizontal angle with relation to the vertical shaft.

This law is clearly illustrated in the accompanying figures, based upon full-size vertical sections of the fore limbs of four types of quadrupeds which exemplify the progressive straightening of the limb, step by step, with progressive increase in bulk and size. (See fig. 668.)

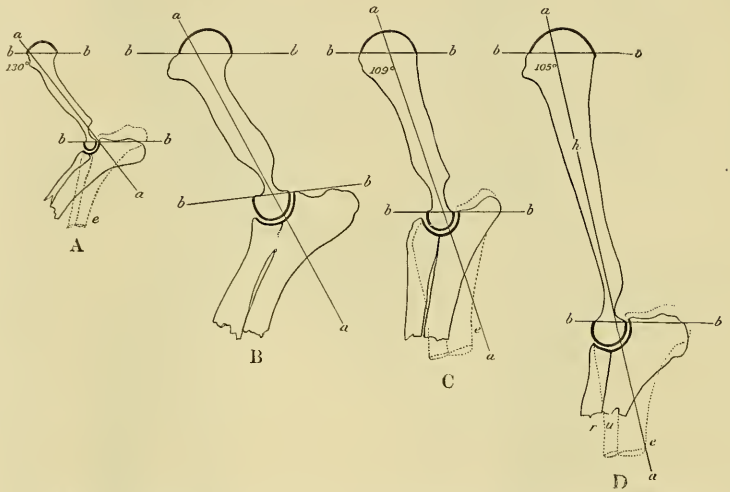


FIGURE 668.—Angulation of the fore limb in graviportal types, as shown by longitudinal sections of the humerus, ulna, and radius

A, *Rhinoceros unicornis;* B, *Brontotherium leidyi;* C, *Eobasileus cornutus;* D, *Elephas indicus.* After Osborn. A, B, Incompletely graviportal adaptations, with the humeroradial angle more acute and the proximal and distal articular facets more oblique to the long axis of the shaft; C, D, advanced graviportal adaptations, with the humeroradial angle more open and the proximal and distal articular facets more horizontal to the long axis of the shaft.

Axes.—The main axis of each limb bone is regarded as the line *a–a*, which passes through the center of the proximal facet and behind the center of the distal articular surfaces. It is noteworthy that the edges (*b–b*) of these proximal and distal articular surfaces are in parallel planes. It will be observed that the angle at the elbow is constantly lessening until in the extreme extension of the elbow joint in the elephant it becomes relatively small.

Facets.—Another important change takes place: the proximal and distal facets, which are out of the line of the main axis of the shaft in *Rhinoceros,* are observed to shift more nearly to the extremities of the shaft in *Elephas.* By these means in the straight-limbed Proboscidea, Dinocerata, and Pyrotheria the proximal articular facet comes to lie almost directly across the top of the shaft, while the distal articular facet similarly lies across the bottom of the shaft.

Angles.—In the progressive adaptation of the titanotheres to increasing weight we observe a similar modification of the primitive angulation; both fore and hind limbs become more vertical. Even in the middle Eocene forms, such as the subgraviportal *Palaeosyops,* the hind limb is exceptionally vertical.

Patella.—The above adaptation is accompanied also by a shifting of the position of the patella. In the primitive, highly flexed ungulate limb the patella is placed at the extremity of the shaft; the patellar facet forms a sharp angle with the axis of the shaft. In the graviportal femur the patella shifts forward to the front of the shaft, and the patellar facet becomes nearly parallel with the long axis of the shaft.

Head of the femur.—In graviportal animals the head of the femur is sessile upon the top of the shaft, so that the weight of the body, in so far as it is represented by the pressure of the acetabulum upon the head of the femur, is transmitted directly through the shaft of the femur (H. F. Osborn). This arrangement, together with the subvertical position of the ilium, the relatively narrow transverse diameter of the pelvis across the acetabula, and the inwardly tilted tibial facet of the femur, brings the feet close to the midline and directly beneath the acetabulum (W. K. Gregory).

INDICES AND RATIOS OF LIMB SEGMENTS IN CURSORIAL AND GRAVIPORTAL UNGULATES (ALLOMETRIC ADAPTATIONS)

RESULTS OF COMPARATIVE STUDIES

The comparative studies pursued by Osborn and Gregory, based upon limb segment measurements taken by Gregory for this monograph in about sixty quadrupeds, bring forth some new and significant laws of limb proportion in addition to those already adumbrated by various students of animal locomotion and of the evolution of quadrupeds. Valuable as have been the previous studies of Marey, Osborn, Gaudry, and others on miscellaneous types, it is only through the measurement and comparison of all the ungulate types in continuous phyletic series, such as are now afforded through American paleontology, that these laws can be positively formulated as fundamental and universal principles of progressive evolution in the limbs.

Antithetic proportions.—In general these measurements show that in extreme graviportal, slow-moving types we have, in the fore limb, humerus long, radius shorter, manus very short; whereas in cursorial, swift-moving types we have humerus short, radius long, manus very long. Similarly in the hind limb we have, in graviportal types, femur long, tibia short, pes very short, whereas in cursorial types we have femur short, tibia long, pes very long.

During the course of evolution small subcursorial types have frequently diverged on the one hand into gigantic graviportal types and on the other hand into true cursorial types. The divergent evolutionary changes may be summarized thus:

	Speed allometry	Weight allometry
Humerus and femur	Shorten.	Lengthen.
Radius and tibia	Lengthen.	Shorten.
Mtc III and Mts III	Lengthen.	Shorten.

Between these extremes we find many intermediate forms. Taken together, the living and extinct quadrupeds may be arranged with reference to primitive or ancestral proportions and to either graviportal or cursorial adaptations into four general groups of types, adapted for various speeds and paces as follows.

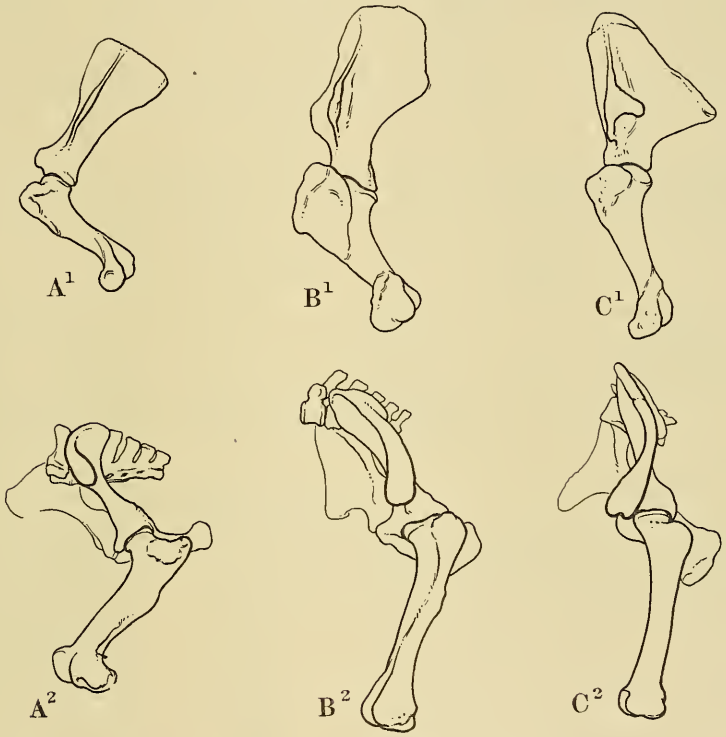


FIGURE 669.—Angulation of the limb bones at the shoulder and hip joints in the standing pose of cursorial (A) and graviportal (B, C) ungulates

A^1, A^2, *Equus scotti*, a Pleistocene horse; B^1, B^2, *Brontops robustus*, an Oligocene titanothere; C^1, C^2, *Mastodon americanus*, a Pleistocene proboscidean. In the cursorial type the humerus is nearly at right angles with the scapula and the femur is nearly at right angles with the ilium. In the graviportal types all the elements become more nearly vertical in position.

Groups of types of quadrupeds adapted to different speeds and paces

Type of locomotion and speed	Type of limb and foot structure	Examples
1. Ambulatory: Small, primitive, low-bodied animals, which walk, shuffle, or run clumsily.	Subplantigrade and spreading; feet short, limbs sharply angulate.	Pantolambda, Hyrax, and many insectivores and carnivores.
2. Mediportal: Speed and pace of intermediate type, tending to become graviportal.	Digitigrade or partly unguligrade; feet secondarily widened; digits of hind foot often reduced in number (from an earlier subcursorial phase), limbs more or less angulate.	Tapirs, titanotheres (Mesatirhinus, Manteoceras), Oligocene rhinoceroses (Caenopus).
3. Graviportal: Gigantic, massive animals, which swing the limbs ponderously in a walk or amble.	Rectigrade; feet very short and wide; phalanges very short, terminal phalanges usually reduced; limbs straight or post-like.	Oligocene titanotheres (Brontotherium), Amblypoda (Coryphodon, Uintatherium), Proboscidea.
4. Cursorial: Swift, light-limbed animals, which leap, gallop, and trot.	Unguligrade; feet very long, narrow, with marked digital reduction; terminal phalanges large; limbs strongly angulate.	Most horses, antelopes, deer, titanotheres (Lambdotherium).

In comparing members of different races or the successive evolutionary stages of a single race we can find in the body no stationary or nonevolving bony segment which will serve as a norm, or fixed standard of comparison: every bone is in a state of change; no segment is constant in length or in proportion to any adjoining segment or to the body as a whole. Nevertheless if we arbitrarily assume that the proximal segment of the hind limb is of the same length (100) in all the animals measured we can then show the relative lengths of the remaining segments of the limb in terms of the length of the femur.

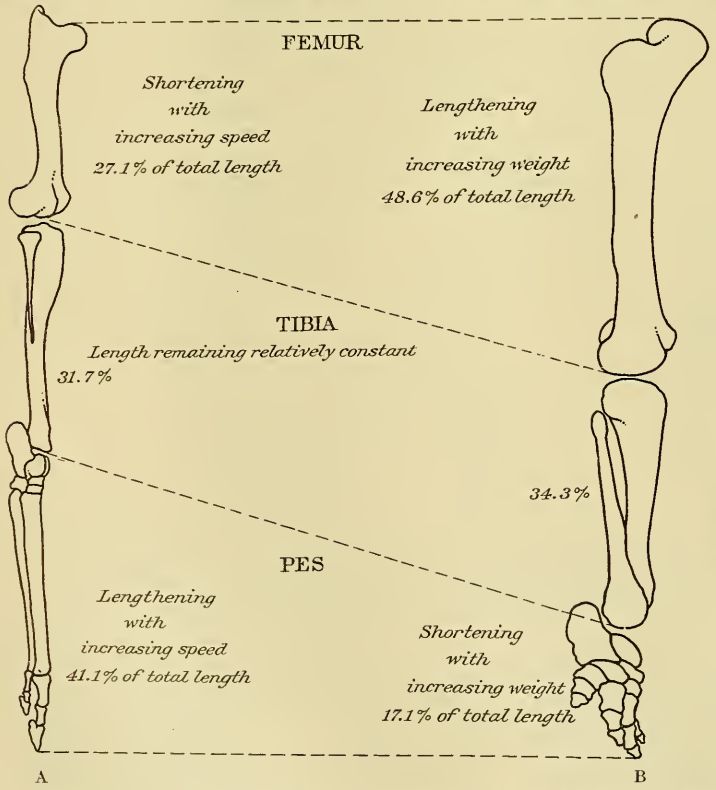


FIGURE 670.—Hind limbs of cursorial and graviportal types, showing adaptive changes in the length of proximal and distal segments

A, Increasing length from proximal to distal segments in a cursorial limb (*Neohipparion*); B, decreasing length from proximal to distal segments in a graviportal limb (*Mastodon*).

Indices.—These are the proportions of a single limb bone, like the femur, or of a single arch element, like the scapula. For our purposes the least breadth of a bone may simply be divided by the greatest articular length and the result expressed as a percentage.

Ratios.—These are obtained between two elements of a limb, as, for example, the length of the tibia divided by the length of the femur gives what may be called the tibiofemoral ratio. This ratio method assumes that every femur or humerus respectively, in being taken as a norm, is reduced to the same absolute length (100). Examples of such ratios are the following:

1. Tibiofemoral ratio = length of tibia ÷ length of femur.
2. Radiohumeral ratio = length of radius ÷ length of humerus.
3. Metatarsofemoral ratio = length of Mts III ÷ length of femur.
4. Metacarpohumeral ratio = length of Mtc III ÷ length of humerus.

Extreme examples of the adaptive range of these ratios in graviportal and cursorial types expressed as percentages, are the following:

Tibiofemoral ratio: Lowest (53) in *Uintatherium mirabile*, a slow, heavy type; highest (125) in *Gazella dorcas*, a swift, cursorial type.

Metatarsofemoral ratio: Lowest (10) in *Uintatherium mirabile*, a graviportal type; highest (103) in *Antilocapra*, a cursorial type.

Radiohumeral ratio: Lowest (52) in *Pyrotherium*, a graviportal type; highest (130) in *Neohipparion whitneyi*, a cursorial type.

Metacarpohumeral ratio: Lowest (18) in *Mastodon*, a graviportal type; highest (144) in *Gazella dorcas*, a cursorial type.

The widest recorded contrasts in limb ratios are as follows:

	Tibio-femoral	Meta-tarso-femoral	Radio-humeral	Meta-carpo-humeral
Giraffa (cursorial)	118	135	160	142
Uintatherium (graviportal)	53	10	70	19

The contrasts between representatives of the chief types of limb adaptation may be further summarized as follows:

	Tibio-femoral	Meta-tarso-femoral	Radio-humeral	Meta-carpo-humeral
Primitive ancestral type, such as Phenacodus primaevus	84	31	87	42
Mediportal intermediate type, such as Palaeosyops leidyi	78	30	72	34
Graviportal digitigrade type, such as Hippopotamus amphibius	67	26	68	38
Graviportal rectigrade type, such as Elephas indicus	60	13	80	22
Cursorial unguligrade type, such as Gazella dorcas	125	81	126	144

The extremes give us what we may popularly designate speed ratios, weight ratios, mediportal ratios, and primitive ratios.

Through convergent evolution animals of different ancestry may come to closely resemble one another in limb ratios, as follows:

	Tibio-femoral	Meta-tarso-femoral	Radio-humeral	Meta-carpo-humeral
Cursorial:				
Perissodactyla, Hipparion (Neohipparion)	117	101	130	116
Artiodactyla (Antilocapra)	123	103	123	130
Graviportal:				
Edentata (Lestodon)	51	12	60	17
Amblypoda (Coryphodon)	61	14	66	19
Brontotheriidae (Brontops robustus)	55	26	82	37
Amynodontidae (Metamynodon)	58	24	81	39
Rhinocerotidae (Teleoceras)	57	25	78	37
Toxodontia (Toxodon)	56	17	77	38

We observe that the tibia is relatively long in the primitive ungulates, probably, as observed above, because of their derivation from unguiculate ancestors, in which the tibia is long. The tibia abbreviates in most heavy, slow-moving types; it elongates in all rapidly moving types.

The radius either remains stationary or abbreviates to a less degree than the tibia in slow-moving types. In swift-moving types the radius appears to elongate as rapidly as the tibia.

The metacarpals and metatarsals progressively abbreviate in graviportal types; they progressively elongate in cursorial types.

RATIOS SHOWING EVOLUTION FROM PRIMITIVE TO GRAVIPORTAL AND CURSORIAL TYPES

The contrasts in the limb segment ratios of these four groups having been shown, it is now necessary to point out some of the common characters of primitive ungulates and to demonstrate the fixed laws of evolution into the graviportal and cursorial extremes as well as the limb segment ratios which prevail in the mediportal types. This may be done in the following comparison of a series of groups of types.

Primitive ungulate types.—The primitive ungulates listed below are partly ambulatory, partly subcursorial, or even cursorial; yet they have in common, as primitive or ancestral characters, the elongate tibia and radius and the primitively abbreviate metatarsus and metacarpus—that is, such animals as *Euprotogonia* and *Eohippus* were undoubtedly cursorial, although they lack the elongate metapodials that are characteristic of modern cursorial types.

Measurements, in millimeters, and ratios of limbs of ungulates of primitive types

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Ambulatory:										
Pantolambda bathmodon	149	114	**76**	36	**24**	124	82	**66**	31	**25**
Meniscotherium terraerubrae	100	91	**91**	29	**29**	82	58	**70**	22	**27**
Subcursorial: Phenacodus primaevus	234	198	**84**	74	**31**	167	146	**87**	70	**42**
Cursorial:										
Euprotogonia puercensis	105	107	**101**	45	**43**					
Eohippus sp	162	162	**100**	[a]82	**50**	121	110	**90**	64	**53**

[a] Estimated.

Phyletic progression (Eocene) to graviportal type.—An extreme instance of progression into the heavy-bodied, slow-moving (graviportal) type is that found in the comparison of the three Amblypoda, *Pantolambda* of the basal Eocene, *Coryphodon* of the lower Eocene, and *Uintatherium* of the upper Eocene. The relative abbreviation of the tibia, of the metatarsus, and of the metacarpus is in contrast with the slight relative elongation of the radius. This illustrates a frequently repeated principle of graviportal adaptation, namely, that the radius is not abbreviated step by step with the tibia but may actually be elongated.

Measurements, in millimeters, and ratios showing progression of Eocene ungulates from the ambulatory to the graviportal type

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Ambulatory: Pantolambda bathmodon	149	114	**76**	36	**24**	124	82	**66**	31	**25**
Graviportal-digitigrade: Coryphodon lobatus	423	260	**61**	62	**14**	363	240	**66**	70	**19**
Graviportal-rectigrade: Uintatherium mirabile	692	360	**53**	70	**10**	540	380	**70**	106	**19**

Primitive cursorial condylarths and perissodactyls.—Even in lower Eocene time the condylarths and perissodactyls embrace many primitive swift and light-limbed types. These cursorial types, which include a lower Eocene titanothere, had what may be called high-speed ratios for the tibia and radius, but low-speed ratios for the metatarsus and metacarpus. The most primitive Eocene titanothere, *Eotitanops*, was subcursorial, and *Lambdotherium* was cursorial in limb proportions, but the material available for these genera does not afford the required indices.

Measurements, in millimeters, and ratios of limbs of primitive cursorial condylarths and perissodactyls

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Phenacodontidae: Euprotogonia puercensis	105	107	**101**	45	**43**					
Lophiodontidae: Heptodon calciculus	175	175	**100**	[a]75	**43**	115	114	**99**	67	**58**
Hyracodontidae: Hyrachyus agrarius	254	243	**95**	110	**43**	197	197	**100**	93	**47**
Equidae: Eohippus sp	167	162	**100**	[a]82	**50**	121	110	**90**	64	**53**

[a] Estimated.

Mediportal or intermediate group.—The mediportal group includes the middle Eocene titanotheres as well as the modern tapirs and some of the older types of rhinoceroses, all animals of intermediate size with an intermediate rate of speed. Here we observe a striking uniformity in the limb segment ratios. As compared with the primitive ungulates shown in the first table above, the mediportal titanotheres were all apparently abbreviating the tibia in connection with their increasing weight. The metatarsals and metacarpals were also abbreviating more rapidly in adaptation to weight. The radius, however, in relation to the humerus, remains relatively long; in several other phyla which are progressing toward the weight-bearing type the radius yields a less constant weight index than the tibia. As indications of speed the tibial and radial are much less reliable than the metapodial indices.

Measurements, in millimeters, and ratios of limbs of mediportal ungulates

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Amynodontidae: Amynodon intermedius	340	[a] 300	71							
Tapiridae:										
Tapirus terrestris	262	208	79	108	41	205	177	86	106	50
Tapirus indicus	320	258	80	120	37	250	228	91	120	48
Titanotheriidae:										
Palaeosyops major	433	332	77	137	31					
Palaeosyops leidyi	370	290	78	110	30	325	235	72	113?	34?
Manteoceras manteoceras	390?	272	69?						[a] 107	
Mesatirhinus petersoni	358	283	79	118	33					
Limnohyops monoconus	387	283	79	123	31	293	228	77	109	37

[a] Estimated.

Phyletic progression to cursorial type in the Equidae.—The above "primitive cursorials" constitute the type from which the "modern cursorials" evolved. The Equidae in their progression into the "modern cursorial" type present exactly the reverse of the graviportal progression seen above in the Amblypoda. They show a relative elongation of the tibia, radius, metatarsus, and metacarpus. After attaining the highest speed ratios in the lower Pliocene *Hipparion* (*Neohipparion*) *whitneyi* we observe a retrogression toward the more heavy-bodied modern *Equus* type and a still greater retrogression into the short-limbed and slow-moving *Hippidion neogaeum* of South America and in the still shorter-limbed *Hyperhippidium*. This is one of the most significant series of comparative ratios which we have obtained.

Measurements, in millimeters, and ratios showing cursorial progression

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Primitive: Eohippus	162	162	100	[a] 82	50	121	110	90	64	53
Intermediate:										
Mesohippus bairdii	170?	170	100?	[a] 98	57?	115?	122	106?	80	69?
Mesohippus sp	178	193	108	121	68	136	[a] 136	100	92	68
Hypohippus osborni	278	277	100	218	78	205	260	127	203	99
Neohipparion whitneyi	249	293	117	252	101	187	244	130	218	116
Equus kiang	313	310	99	277	88	237	302	127	238	100
Equus caballus "Elmer Weeks"	392	363	92	288	73	305	363	119	240	78
Equus scotti	370	330	88	263	71	289	342	118	243	84
Retrogressive: Hippidion neogaeum	340	305	89	214	62	273	287	105	198	72

[a] Estimated.

Cursorial light-bodied artiodactyls.—These animals are convergent with or analogous to the Equidae, yet in the elongation of the tibia they surpass even the *Hipparion* (*Neohipparion*) ratios and attain in *Gazella* and *Antilocapra* the highest speed ratios known. The list is as follows:

Measurements, in millimeters, and ratios of limbs of cursorial artiodactyls

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Primitive:										
Eotylopus reedi	148	142	96	72	52	118	100	84	68	57
Tragulus napu	94	103	109	62	66	74	62	83	42	56
Forest-living: Odocoileus hemionus	253	295	116	255	100	198	223	112	208	105
Plains-living:										
Antilope cervicapra	183	223	121	183	100	133	168	126	180	135
Antilocapra americana	210	260	123	218	103	164	202	123	213	130
Gazella dorcas	140	176	125	132	81	93	118	126	134	144

Subcursorial deep-bodied artiodactyls.—There are two types, ancient and modern, which have strikingly similar ratios. These are the Oligocene *Oreodon* and the modern *Sus*.

Measurements, in millimeters, and ratios of limbs of subcursorial artiodactyls

	Femur	Tibia	Tibio-femoral ratio	Mts III	Meta-tarso-femoral ratio	Humer-us	Radius	Radio-humeral ratio	Mtc III	Meta-carpo-humeral ratio
Oreodon culbertsoni	161	142	**88**	62	**38**	138	113	**81**	57	**41**
Sus scrofa	248	215	**86**	86	**34**	208	168	**80**	77	**37**

Cursorial heavy-bodied artiodactyls.—These relatively heavy-bodied animals were for the most part derived from light-limbed and light-bodied cursorial and subcursorial ancestors. This is positively known to be true of the ancestry of the camels. They therefore are to be compared with the heavy-bodied cursorial Equidae as representing a retrogression from the high-speed ratios of the ancestral light-bodied forms. The excessively long limbs and high limb ratios of the giraffe are doubtless an adaptation to the peculiar feeding habits.

Measurements, in millimeters, and ratios of limbs of cursorial artiodactyls

	Femur	Tibia	Tibio-femoral ratio	Mts III	Meta-tarso-femoral ratio	Humer-us	Radius	Radio-humeral ratio	Mtc III	Meta-carpo-humeral ratio
Plains-living:										
Camelus arabicus	470	400	**80**	325	**66**	363	455	**83**	330	**56**
Bison bison	369	355	**96**	243	**65**	290	293	**101**	198	**60**
Giraffa camelopardalis	466	550	**118**	630	**135**	435	698	**160**	618	**142**
Forest-living: Cervus megaceros	430	454	**105**	350	**71**	334	358	**107**	342	**102**

Graviportal short-limbed digitigrades.—These animals are directly derived from ancestral mediportal digitigrades through increasing weight of body and reduction in the length of the limbs. They are not short-footed but medium-footed, or mesatipodal. Three of them (*Teleoceras, Metamynodon, Hippopotamus*) are or probably were aquatic or amphibious.

Measurements, in millimeters, and ratios of limbs of graviportal digitigrades

	Femur	Tibia	Tibio-femoral ratio	Mts III	Meta-tarso-femoral ratio	Humer-us	Radius	Radio-humeral ratio	Mtc III	Meta-carpo-humeral ratio
Toxodon sp	577	325	**56**	101	**17**	387	298	**77**	147	**38**
Teleoceras fossiger	408	233	**57**	105	**25**	[a] 305	238	**78**	114	**37**
Metamynodon planifrons	480	280	**58**	118	**24**	393	320	**81**	153	**39**
Hippopotamus amphibius	498	332	**67**	130	**26**	395	270	**68**	152	**38**

[a] Estimated.

Graviportal long-limbed digitigrades.—The Oligocene titanotheres are the only known quadrupeds of this type. They are distinguished by being relatively long-limbed in contrast with the short-limbed group just described and with the mediportal and graviportal rhinoceroses. A striking fact is that the limb ratios are very similar to those in the low-bodied, short-limbed class above described. Thus the ratios remain the same in low-bodied and high-bodied heavy forms of moderate speed. It is noteworthy that the hind limb of the titanotheres parallels that of the elephant or rectigrade group and is quite unlike that of the other graviportal digitigrades.

Measurements, in millimeters, and ratios of limbs of Oligocene titanotheres

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-humeral ratio	Mtc III	Metacarpo-humeral ratio
Brontotherium gigas	780	427	**54**	200	**20**	528	478	**90**	214	**40**
Menodus trigonoceras	770	430	**55**	[a] 220	**28**	620	520	**83**	240	**38**

[a] Estimated.

Graviportal rectigrades.—The graviportal rectigrades are heavy-bodied, long-limbed, short-footed (brachypodal) quadrupeds, typified by the elephants. The type has been called by Gaudry "rectigrade." We do not yet know the stages of graviportal progression in the evolution of the Proboscidea. Our knowledge of these stages must be gained by a comparison of the ancestral series, which is still incomplete. The measurements given below show the relatively short tibia and radius and the very short metatarsus and metacarpus, which are paralleled by those of the graviportal Amblypoda and Pyrotheria.

Measurements, in millimeters, and ratios of limbs of graviportal rectigrades

	Femur	Tibia	Tibio-femoral ratio	Mts III	Metatarso-femoral ratio	Humerus	Radius	Radio-bumeral ratio	Mtc III	Metacarpo-humeral ratio
American mastodon (Mastodon americanus)	[a] 1, 020	705	**69**	117	**11**	885	670	**75**	165	**18**
Indian elephant (Elephas indicus)	1, 020	618	**60**	138	**13**	810	685	**80**	183	**22**
African elephant (Loxodonta africanus)	1, 050	755	**71**	144	**13**	------	870	**87**	205	**20**
Uintatherium mirable (Eocene)	695	360	**53**	70	**10**	540	380	**70**	106	**19**
Pyrotherium sp. (Eocene)	622	351	**56**	------	------	452	238	**52**	------	------

[a] Estimated.

SUMMARY OF CURSORIAL AND GRAVIPORTAL PROPORTIONS OF SEGMENTS OF LIMBS OF UNGULATES

FEATURES CONSIDERED

The foregoing principles of evolution of the ungulate limbs are again illustrated in the widely varying types of locomotion comprised within the nine typical families of the great order Perissodactyla. These families range from the extreme cursorial to the extreme graviportal adaptation. A still more remarkable fact is that within several single families both extremes of adaptation are developed. The habits and habitats of these families and subfamilies are treated in Chapters I (Preliminary), II (Adaptive radiation), X (Origin and evolution), and VIII (Musculature of titanotheres and other Perissodactyla) of this monograph.

We may now examine the perissodactyls in respect to the length, proportions, and other adaptive features of the scapula, humerus, radius, ulna, ilium, femur, tibia, and fibula.

The student who desires to acquaint himself with the muscles which control the shifting rugose areas of origin and insertion should consult Chapter VIII.

The foregoing summaries and comparisons of limb ratios in the ungulates generally help to a comprehension of the adaptations of the arches and limbs of the titanotheres and other Perissodactyla, because these animals naturally parallel members of other groups of ungulates.

The arch and limb elements of the Perissodactyla are displayed in the following synoptic figures:

Figures 671–673. Condylarthra and Perissodactyla.
Figure 674. Artiodactyla and Perissodactyla.
Figures 675, 676. Lophiodontidae (Helaletinae) (subcursorial).
Figure 676. Tapiridae (mediportal).
Figure 678. Palaeotheriidae (cursorial to mediportal).
Figure 679. Hyracodontidae (subcursorial).
Figure 679. Amynodontidae (mediportal to graviportal).
Figures 679–682. Rhinocerotidae (subcursorial to graviportal).
Figures 683, 684. Equidae (cursorial).
Figures 685, 686. Brontotheriidae (mediportal to graviportal).

A comparative survey of these figures bone by bone or segment by segment demonstrates afresh that in each family respective adaptations to mediportal, to graviportal, or to cursorial locomotion results in convergent, parallel, or homoplastic forms, proportions, ratios, and indices.

Under this masterful influence of teleogeny, or analogous adaptation, which masks, dominates, or completely conceals the syngenetic or ancestral characters, there still remain two causes of distinction or separation between members of different phyla:

(1) Certain features of original, or syngenetic resemblance survive; (2) the adaptation of structure is rarely exactly analogous, because the functions or movements of the limbs in two unrelated forms are rarely, if ever, exactly analogous.

For example, the mediportal titanothere *Mesatirhinus* may imitate the mediportal *Tapirus;* the resulting limb proportions and forms are closely but not exactly similar. Likewise the femur of the graviportal *Brontotherium* is not exactly similar to that of any other known graviportal form. The differences are due to differences in the gait, step, or mode of progression, as well as to the syngenetic influence of the ancestral forms from which these types respectively converged.

FORMS OF SCAPULA

That the proportion and form analogies, if not exact, are very close, is demonstrated over and over again in almost any bone we may select. For example, in the scapula there are three chief forms, which are produced repeatedly in different families—namely, the "mediportal," the "graviportal," and the "cursorial."

The primitive scapula of *Phenacodus* is a suboval type from which that of *Tapirus*, *Mesatirhinus*, and other primitive mediportal scapulae are readily derived. A feature of the primitive scapula is the prominent acromial process of the spine, which is retained in the amblypod *Uintatherium* but lost in most

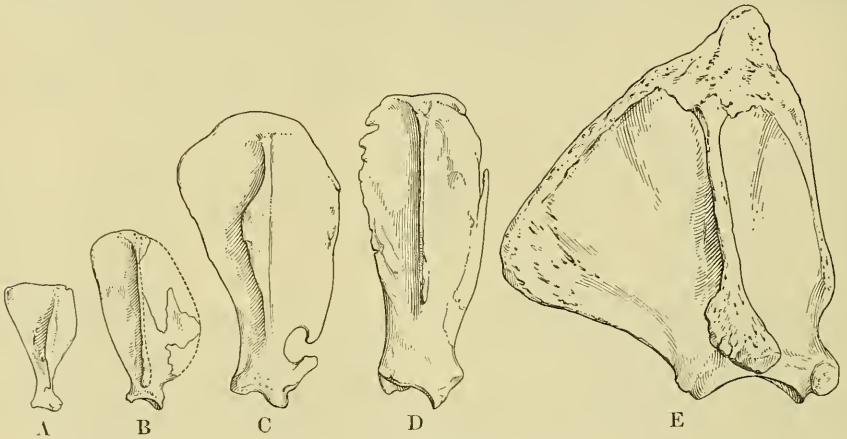


FIGURE 671.—Five types of scapula

A, Cursorial (*Mesahippus*); B, primitive (*Phenacodus*); C, mediportal (*Tapirus*); D, heavy mediportal (*Palaeotherium*); all one-sixth natural size. E, Graviportal (*Uintatherium*); one-eighth natural size.

The general contrast in the form and proportions of the limb segments between cursorial and graviportal types may be summarized as follows:

Contrast between cursorial and graviportal types

Arch and limb elements	Cursorial	Graviportal
Neck of scapula	Contracted.	Expanded.
Blade of scapula	Lengthened.	Broadened.
Axis of pelvis	More horizontal.	More vertical.
Axis of humerus and femur	More horizontal.	More vertical.
Muscular insertions on humerus and femur.	Raised.	Lowered.
Femur and humerus	Abbreviated.	Elongated.
Tibia and radius	Elongated.	Abbreviated.
Mts III and Mtc III	Elongated.	Abbreviated.
Tuberosity of humerus	Abbreviated.	Elongated.
Great trochanter on femur	Elongated.	Abbreviated.

Perissodactyla, in which we observe a prominent tuber spinae.

The mediportal scapula, as illustrated in *Tapirus*, with graviportal variations seen in *Palaeotherium magnum* and in *Rhinoceros unicornis*, is ovate, elongate, with rounded superior border and with equally developed fossae for the supraspinatus and infraspinatus muscles.

The graviportal scapula as illustrated in *Metamynodon*, *Teleoceras*, and *Brontotherium* is, on the contrary, trihedral, with a broad angulate extension of the posterior border for the infraspinatus muscles. Its analogies are with the scapulae of *Elephas*, *Uintatherium*, and other large graviportal animals.

The cursorial scapula as illustrated in *Neohipparion*, *Antilocapra*, *Hyracodon*, of speed type, is long-necked, fan-shaped—that is, expanded above—with progressive enlargement of the infraspinous fossa and corresponding diminution of the supraspinous fossa; the superior border is truncate rather than rounded or angulate.

The evolution of the scapula is analogous to that of the ilium, chiefly in the following respects: (1) Length of the neck or peduncle; (2) distance between the areas of origin and insertion of the muscles; (3) breadth or contraction of the superior border; (4) support of thorax by scapula as compared with support of viscera by ilium.

Comparison of mediportal, graviportal, and cursorial types of ungulates

Mediportal	Graviportal	Cursorial
Scapula elongate, suboval or quadrate; upper border rounded. Neck elongate but not constricted. Tuber spinae persistent. Prespinous and postspinous fossae of equal size.	Scapula depressed, subtriangular; upper border acute. Neck sessile or abbreviate. Tuber spinae expanded. Postspinous fossa triangular or expanded superiorly.	Scapula vertically elongated triangle; upper border truncate. Neck elongate and constricted. Tuber spinae reduced. Prespinous fossa reduced.
Examples: Palaeosyopinae, Tapiridae, Palaeotheriidae, Oligocene Rhinocerotidae.	Examples: Brontotheriinae, Amynodontidae, Rhinocerotidae (teleocerine).	Examples: Equidae, Hyracodontidae, cursorial Palaeotheriidae (Paloplotherium minus), subcursorial Lambdotheriinae.

FORMS OF HUMERUS

The distal end of the humerus is a highly distinctive region in the ungulates because of the profound changes of function in the passage from the ancestral unguiculate type, in which the manus has powers of pronation and supination, to the specialized ungulate type, in which the manus is restricted to flexion and extension. The progress of this change of function is reflected in the structure of the distal articular surface of the humerus (rotula, capitellum) and of the inner and outer rugosities for the muscular attachments, which are known as the entocondylus and ectocondylus. The ancestral ungulate arrangement of these condyles is as follows:

Region of entocondyle, for the attachment of internal ligament, pronator teres muscle (reduced), flexor carpi radialis muscle, flexor profundus digitorum muscle, flexor sublimis digitorum muscle, palmaris longus muscle.

Region of ectocondyle, for the attachment of external ligament, supinator longus muscle,[50] extensor communis digitorum muscle, extensor minimi digiti muscle, extensor carpi ulnaris muscle.[51]

In the passage from the unguiculate to the ungulate type we observe the following general laws of transformation of the ectocondyle, entocondyle, and rotula:

(1) All primitive ungulates (such as *Periptychus, Phenacodus, Meniscotherium, Coryphodon, Uintatherium*) inherit a large entocondyle and a relatively small ectocondyle.

(2) In all higher ungulates this condition is exactly reversed: the entocondyle is reduced or wanting, the ectocondyle is greatly enlarged.

(3) In quadrupeds of intermediate size, or mediportal types (such as *Tapirus*), the entocondyle and ectocondyle are equally developed.

Thus the greatest muscular rugosities of the primitive graviportal *Coryphodon* are entocondylar, or on the inner side of the lower end of the humerus, whereas the greatest muscular rugosities of the progressive graviportal *Rhinoceros* are ectocondylar. In other words, there is a transfer of the balance of muscular power from the inner pronator and flexor side of the limb to the outer supinator and extensor side, together with a change of function of the extensor carpi ulnaris into a flexor of the forefoot (Windle and Parsons, 1901.1, pp. 700, 701).

In the meantime the distal articular extremity of the humerus, which is primitively composed of the rotula for the ulna and capitellum for the radius, an asymmetric arrangement, becomes a more symmetric joint. This symmetry of the inner and outer sides is attained only in the highly specialized cursorial elbow joint of *Equus*, which is strictly limited to flexion and extension.

These four types of humeral adaptation may be summarized and contrasted as follows:

Types of humeral adaptation

	Primitive ungulate (e. g., Phenacodus)	Intermediate mediportal (e. g., Tapirus)	Graviportal (e. g., Rhinoceros)	Cursorial (e. g., Equus)
Entocondyle	Large.	Medium.	Greatly reduced.	Reduced.
Ectocondyle	Medium.	Medium.	Greatly enlarged.	Reduced.
Rotula and capitellum	Asymmetric.	Asymmetric.	Asymmetric.	Symmetric.

[50] Arises from the supinator crest above the ectocondyle. The supinator brevis is absent or vestigial in ungulates. It originally arose partly from the ectocondyle (Windle and Parsons, 1897.1, p. 402; 1901.1, p. 701).

[51] Serves as a flexor of the carpus in ungulates (Windle and Parsons, 1903.1, p. 391).

The distal end of the humerus is thus highly distinctive as between cursorial or graviportal function. It exhibits in the mediportal *Tapirus* a balanced condition of muscular attachment upon the entocondyle and ectocondyle; similarly the deltoid crests are moderately developed and the tuberosities are high.

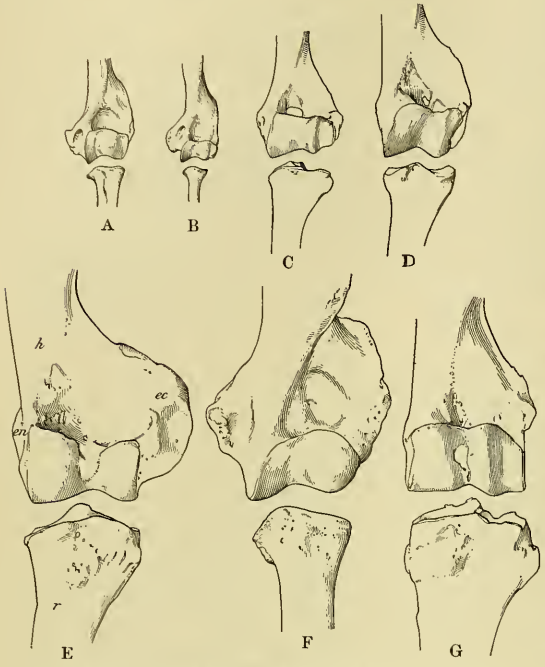


FIGURE 672.—Forms of distal articular surface of humerus

A, Primitive (*Phenacodus*); B, primitive (*Pantolambda*); C, mediportal (*Tapirus*); D, subgraviportal (*Limnohyops*); E, graviportal digitigrade (*Rhinoceros*); F, graviportal rectigrade (*Coryphodon*); G, cursorial (*Equus*). All one-third natural size.

A marked characteristic of graviportal adaptation is the rapid development of the ectocondylar crest and of the extensor carpi radialis muscle; this development is initiated in *Palaeosyops* and is carried to an extreme in *Rhinoceros* and the later titanotheres. The entocondylar process diminishes, and the humeral trochleae are oblique, asymmetrical.

In cursorial types like the Equidae neither the entocondyle nor ectocondyle relatively increases, obviously because the lateral or pronating and supinating movements are almost wholly replaced by orthal or extensor and flexor movements. In cursorial forms the humeral trochlear convexities become vertical; in graviportal forms they remain oblique.

ANALOGOUS ADAPTATION IN HUMERUS AND FEMUR

Reviewing the following series of comparative figures and descriptions of the limbs of the ungulates, and especially of the perissodactyls, we deduce certain laws of transformation and transposition of areas of muscular attachment that are almost as constant as the allometric linear changes of proportion set forth in section 1 of this chapter.

Analogous principles of cursorial and graviportal adaptation operate in general in the fore and hind limbs, but there are some exceptions. The most striking contrast is observed in the muscular attachments at the upper end of the humerus and femur respectively.

In graviportal progression the tuberosities of the humerus are raised and expanded and the analogous great trochanter of the femur is lowered and depressed. Conversely, in cursorial progression the tuberosities of the humerus are lowered and depressed and the great trochanter of the femur is raised and expanded.

The chief divergences and parallelisms between the transformations of the humerus and femur are shown in the accompanying table.

Divergences and parallelisms in the transformation of the humerus and femur in ungulates

Adaptation	Humerus	Femur
Mediportal	Of medium length; equal to or exceeding the radius. Great tuberosity above level of head. Deltoid crest on upper third of shaft. Entocondylar and ectocondylar crests subequal. Elbow flexed.	Of medium length; equal to or exceeding the tibia. Great trochanter above level of head. Third and second trochanters on upper third of shaft. Knee flexed.
Graviportal	Oblique. Elongate as compared with radius. Great tuberosity expanding and elevated. Deltoid crest expanding and lowered on shaft. Ectocondylar crest enlarged (entocondylar crest relatively reduced). Olecranon of ulna depressed. Elbow less flexed.	Oblique or vertical. Elongate as compared with tibia. Great trochanter depressed. Third trochanter expanding and lowered on shaft. Second trochanter sessile. Knee less flexed or straight.
Cursorial	Abbreviate as compared with radius. Great tuberosity not elevated. Deltoid crest rather high on shaft. Ectocondyle and entocondyle reduced. Elbow flexed.	Abbreviate as compared with tibia. Great trochanter erect, elevated. Third and second trochanters high on shaft. Knee flexed.

FORMS OF ILIUM

In the evolution of the ilium, as in the evolution of the scapula, teleogenetic or analogous adaptation to weight or to speed is far more potent and conspicuous than ancestral influence. Of the ilium, as of the scapula, there are four main types, the primitive (such as that of *Phenacodus*), the mediportal (*Tapirus*), the graviportal (*Titanotherium*, *Elephas*), and the cursorial (*Neohipparion*). These four types are fashioned by the demands of the musculature and the movements of the limbs.

The ilium of titanotheres of the early graviportal type (*Manteoceras*) and of the advanced graviportal type (*Brontops*) is analogous to that of the heavy, slow-moving rhinoceroses (*Metamynodon*, *Teleoceras*). It presents wide differences from the ilia of extremely cursorial types, such as *Hyrachyus*, *Mesohippus*, and *Equus*.

The general contrast is shown below:

Cursorial characters	Graviportal characters
Supra-iliac border narrow, concave.	Supra-iliac border broad, continuously arched, convex.
Tuber coxae and tuber sacrale separated by long, thin crista iliaca.	Tuber coxae and tuber sacrale continuous, rugose.
Ilium relatively narrow and long.	Ilium short, spreading.
Iliac peduncle narrow, long.	Iliac peduncle broad, short.

Five types of ilia are illustrated in A, B, C, D, and E of Figure 673:

1. The primitive hypothetical ancestral form is shown in A.
2. The superior border of the ilium of all the early Eocene perissodactyls, so far as known, exhibits the subcursorial form shown in B.
3. The Eocene titanotheres fall into the incipient or subgraviportal form E, which represents a considerable advance on the ilium of *Tapirus*. It is an intermediate form, with greatly broadened ilia, but still exhibits the interrupted superior border *b*.
4. The Oligocene titanotheres fall into the extreme graviportal form F, with greatly expanded iliac border. This is the extreme weight-bearing type.
5. The Equidae exhibit an extreme cursorial form (D) in *Equus*.

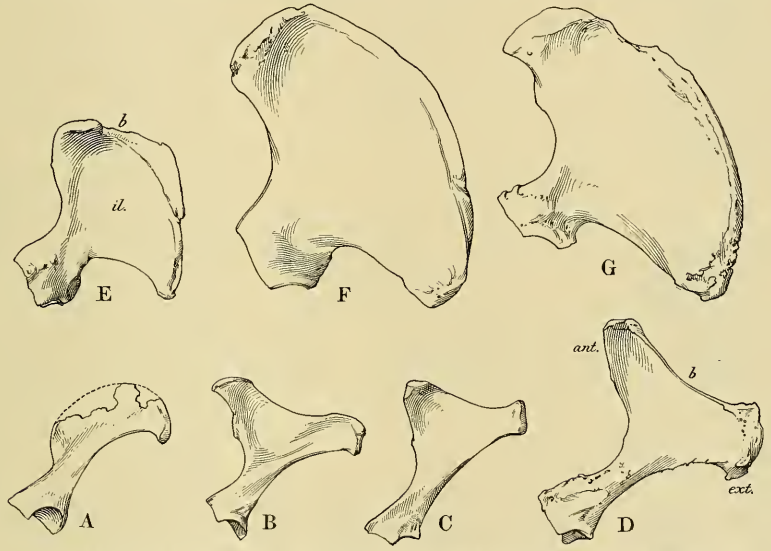


FIGURE 673.—Seven typical forms of ilia, showing cursorial and graviportal adaptations

A, Primitive subcursorial (*Phenacodus*), one-sixth natural size; B, cursorial (*Hyrachyus*), one-sixth natural size; C, cursorial (*Mesohippus*), one-fourth natural size; D, extreme cursorial (*Equus*), one-eighth natural size; E, subgraviportal (*Manteoceras*), one-eighth natural size; F, graviportal (*Brontops*), one-twelfth natural size; G, graviportal (*Teleoceras*), one-eighth natural size.

To understand the evolution of the ilium we must distinguish between the crests (cristae) or borders and the fossae areas or surfaces, starting with the primitive mammalian ilium (A) and following the progressive changes in the main attachments for the abdominal muscles and the flexors and extensors of the limbs. The actual transitions between this primitive mammalian (A) of condylarthrous or unguiculate type and the oldest mediportal ungulate type are not known, so that the comparisons made below are somewhat conjectural.

It is noteworthy that whereas there is a wide contrast in the scapulae of *Tapirus* (mediportal) and of *Equus* (cursorial), the ilia of the same animals are not greatly different in form (fig. 674).

1. In the mediportal ilium of *Tapirus cc* (tuber coxae) corresponds broadly with the primitive anterior border of the ancestral ilium of the unguiculates and condylarths (A). It serves chiefly for the attachment of the obliquus abdominis externus and o. a. internus muscles.

3. As compared with the even border of the unguiculate, creodont, or condylarth ilium the raised border *ss* (tuber sacrale) appears to be a neomorph, or secondary upgrowth of the suprasacral border of the ilium, designed on the dorsal fossae for the expansion of the gluteus medius and longissimus dorsi muscles,

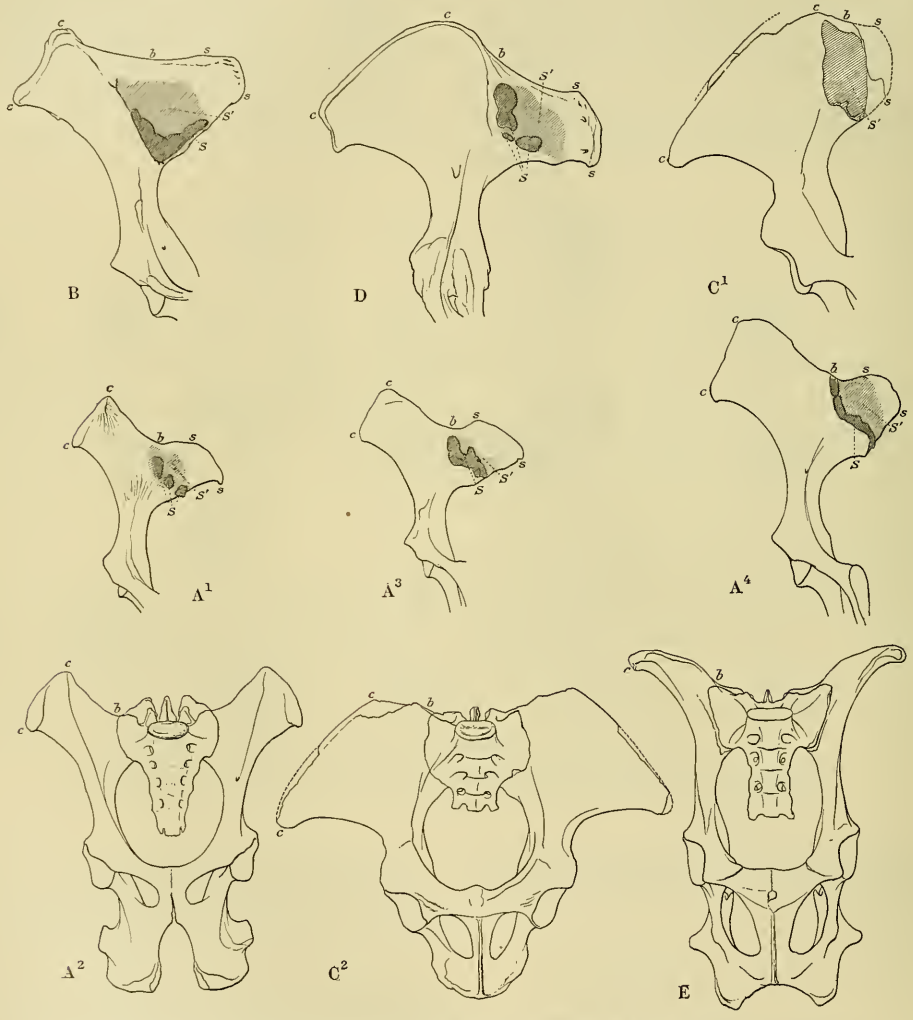


FIGURE 674.—Adaptive forms of ilia and sacral attachment

A¹–A⁴, Mediportal (A¹, A³, *Tapirus terrestris*, juv.; A³, the same, adult; A⁴, *T. indicus*, adult); B, cursorial (*Equus*); C¹, subgraviportal (*Manteoceras*); C², the same with sacrum; D, graviportal (*Rhinoceros*); E, cursorial (*Rangifer*). *S*, Sacral attachment; *S'*, suprasacral fossa; *ss*, tuber sacrale; *cc*, tuber coxae; *b*, region between *ss* and *cc*. All two-fifteenths natural size.

2. The smooth, thin intermediate crista *cs* broadly compares with the dorsal border of the primitive ilium and is mainly for the insertion of the fascia of the longissimus dorsi, a muscle which is much more important in the ungulates than in the unguiculates. and on the ventral side for the ligamentous fixation of the pelvis to the sacrum. The gluteus medius, with its profound insertion in the great trochanter (t′) and third trochanter (t‴) of the femur, is one of the most important propellers of the heavy ungulate body.

4. The antero-inferior or ventral triangular surface (fossa iliaca) serves mainly for the attachment of the iliacus muscle, a flexor of the femur which is inserted into the second trochanter (t'').

Starting with this interpretation of the adaptation of the bony surfaces of the ilium to its muscular functions we observe the following simple principles: (1) The expansion of the borders *cc* and *ss* is greater or less according to the respective development of weight or of speed; (2) thus in cursorial types such as the Equidae the borders *cc* and *ss* remain relatively narrow, while the thin crista iliaca between them remains relatively broad; (3) the expansion of the border *ss* and of the adjacent suprasacral fossa for the attachment of the gluteus medius muscles is a universally progressive character in mediportal and graviportal ungulates and is seen in different degrees in *Tapirus, Equus, Rhinoceros, Palaeosyops,* and other Perissodactyla, but it is relatively far more marked in the graviportal Artiodactyla (such as *Hippopotamus*) than in the Perissodactyla; (4) the expansion of the border *cc* is also universal in mediportal and graviportal quadrupeds (*Amynodon, Rhinoceros, Brontotherium*) with a heavy abdomen and large abdominal muscles; (5) thus the primitive concave superior border *cs* or crista iliaca is contracted (*Rhinoceros*) and then obliterated by the expansion of the rugose borders *cc* and *ss*, which finally become confluent and form a continuous arch.

All the most ancient perissodactyls, such as *Eohippus, Hyrachyus,* and even *Amynodon,* exhibit a flat or concave crista iliaca between the tuber coxae (*cc*) and the tuber sacrale (*ss*). In such cursorial and subcursorial types of ilium with concave or interrupted superior border (crista iliaca) there is an extension of the gluteal muscles forward to unite with the fibers of the longissimus dorsi, making possible the gallop. In primitive artiodactyls also this flat or concave superior border, or crista iliaca, is older than the convex superior border, because the subcursorial stage always appears to antedate the graviportal stage.

The rounding out of the superior border (crista iliaca) of the ilium which accompanies the expansion of the gluteal abdominal muscles is proved to be a progressive or secondary character by the comparison of a great number of mediportal with succeeding graviportal types of animals. For example, we may compare the lower Oligocene *Caenopus* with the upper Miocene *Teleoceras* (fig. 673, G). Again, we may compare the mediportal upper Eocene *Amynodon* with the graviportal Oligocene *Metamynodon,* or the incipient graviportal Eocene *Palaeosyops* with the Oligocene *Brontotherium.* Thus the broad spreading and convex superior border is correlated with the vertically placed pelvis and elongate femur of such graviportal forms as *Brontotherium* and the rectigrade *Elephas;* it is correlated with the slower gait and with heavy abdominal muscles.

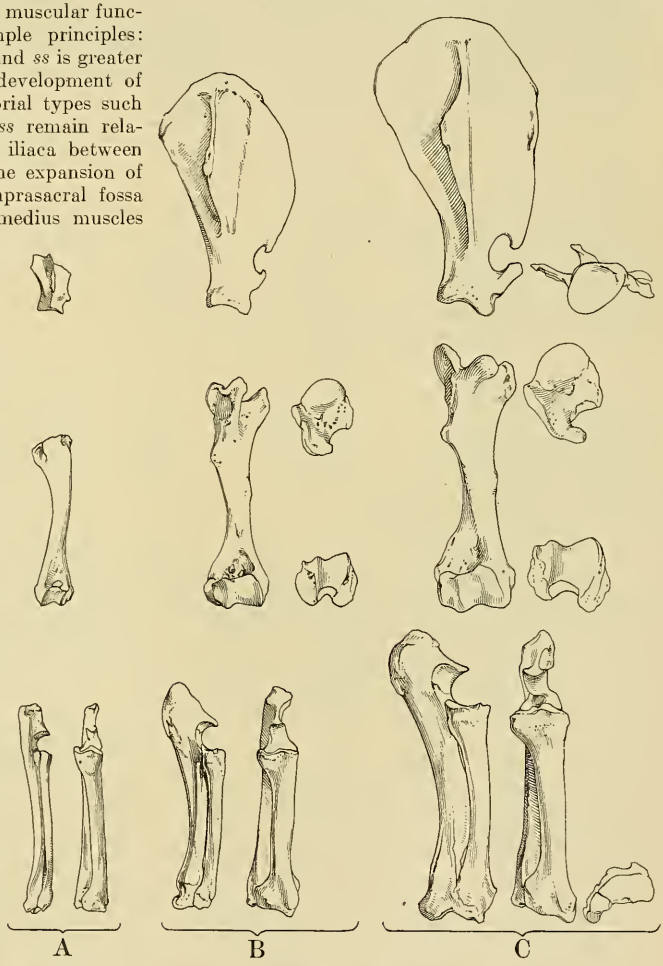


FIGURE 675.—Limb structure of perissodactyls: Fore limbs of *Heptodon* and *Tapirus* A, *Heptodon calciculus* (family Lophiodontidae), one-fourth natural size; B, *Tapirus terrestris,* and C, *Tapirus indicus* (family Tapiridae), one-sixth natural size. Showing the contrast between a primitive lower Eocene cursorial type (*Heptodon*) and a persistent modern mediportal type (*Tapirus*).

LENGTH OF ILIUM AND OF ISCHIUM AND RATIO OF THESE LENGTHS TO TOTAL LENGTH OF OS INNOMINATUM

The absolute length of the ilium measured from the middle of the superior crest to the center of the acetabulum, the length of the ischium, and the ratio of these lengths to that of the os innominatum in certain mediportal, cursorial, and graviportal types are shown in the following table:

Lengths of ilium and of ischium and their ratio to length of os innominatum in certain Perissodactyla and Artiodactyla

[Measurements in millimeters; ratios in percentage]

	Ilium		Ischium		Length of os innominatum
	Length	Ratio	Length	Ratio	
PERISSODACTYLA					
Tapirus terrestris, juvenile (mediportal)	182	56	141	44	323
Tapirus terrestris, adult (mediportal)	200	56	158	44	358
Tapirus indicus (mediportal)	258	60	169	40	427
Equus caballus (cursorial)	290	60	190	40	480
Rhinoceros (Opsiceros) bicornis (graviportal)	330	62	200	38	530
Manteoceras manteoceras (Am. Mus. 2358) (graviportal)	285	67	140	33	425
ARTIODACTYLA					
Tragulus (subcursorial)	56	50	55	50	111
Sus (subcursorial)	134	50	129	50	263
Cervulus	84	53	74	47	158
Auchenia lama (cursorial)	146	53	129	47	275
Dicotyles (subcursorial)	118	55	95	45	213
Hippopotamus amphibius (graviportal)	370	55	300	45	670
Camelus dromedarius, juvenile (cursorial)	207	61	130	39	337

This table shows that we can not at present establish any law or make any deduction as to these ratios with reference to speed and weight, but it brings out two facts of interest: First, the ilium as compared with the ischium is proportionately longer in the Perissodactyla than in the Artiodactyla; second, the ilium of the titanotheres is proportionately longer than in other Perissodactyla.

The true cursorial, mediportal, and graviportal indices are obtained by dividing the entire length of the pelvis (from crest of ilium to extremity of ischium) by the entire breadth (across the widest part of ilium). In the graviportal type the pelvis is short and broad; in the cursorial type it is long and narrow.

RATIOS OF LENGTH OF SCAPULA AND ILIUM TO THAT OF HUMERUS AND FEMUR, RESPECTIVELY

From the constancy of the limb-segment ratios in graviportal and cursorial forms it was expected that somewhat similar ratios would be discovered between the arch elements and the proximal limb segments. For example, in the graviportal Proboscidea the ilium shortens and expands while the femur lengthens; conversely in the cursorial Equidae the scapula lengthens while the humerus shortens.

To ascertain whether there is any law underlying these allometric changes Gregory made a test series of comparative measurements and obtained the following ratios, expressed as percentages (scapula ÷ humerus = scapulohumeral ratio; ilium ÷ femur = ilio femoral ratio):

Ratio of length of scapula and ilium to length of humerus and femur

	Scapulo-humeral ratio	Ilio-femoral ratio
Phenacodus primaevus (primitive)	109	65
Phenacodus wortmani (primitive)	104	61
Coryphodon lobatus (graviportal)	------	82
Mastodon americanus (graviportal, rectigrade)	93	62
Elephas indicus (?)	94	56
Elephas africanus (graviportal, rectigrade)	88	54
Toxodon (graviportal, digitigrade)	150	------
Palaeosyops leidyi (mediportal to graviportal)	107	74
Palaeosyops major (mediportal to graviportal)	------	66
Brontotherium gigas (mediportal to graviportal)	121	66
Hyrachyus agrarius (cursorial)	------	52
Hyracodon nebrascensis (cursorial)	114	------
Amynodon intermedius (mediportal)	------	73
Metamynodon planifrons (graviportal)	------	61
Teleoceras fossiger (graviportal)	------	78
Rhinoceros indicus (graviportal)	118	74
Mesohippus (cursorial)	108	60
Hypohippus (cursorial)	120	66
Neohipparion (cursorial)	131	77
Equus scotti (cursorial)	118	75
Equus caballus (cursorial)	120	60
Hippidion (subcursorial)	132	77
Cervus megaceros (cursorial, heavy-bodied)	140	83
Bison bison (cursorial, heavy-bodied)	140	------
Camelus arabicus (cursorial, heavy-bodied)	113	------
Antilocapra (cursorial)	112	------

This table appears to show that there is no constant significance in the ratios of length between the scapula and the humerus. In the Equidae, for example, the scapula appears to be elongating with speed as we pass from *Mesohippus* to *Neohipparion*, but the scapula of the slow-moving *Hippidion* exceeds in length that of the swift *Neohipparion*, and both are surpassed by that of *Toxodon*. Similarly the abbreviation of the ilium as compared with the elongation of the femur reveals no contrast of speed or weight ratios.

The indices, or relations of breadth to length, of the ilium and scapula respectively afford the really significant and important figures.

SECTION 2. SYSTEMATIC COMPARISON OF THE PECTORAL AND PELVIC ARCHES AND OF THE LIMB BONES IN EIGHT FAMILIES OF PERISSODACTYLS

TAPIRIDAE AND LOPHIODONTIDAE

THE TAPIRS

In limb proportions the modern tapirs (*Tapirus*) are typical persistent mediportal types. Even at the present time they are in an earlier stage of evolution than the light-limbed Eocene titanotheres (*Mesatirhinus*); and they are also capable of more rapid motion, as indicated by the greater length of the metapodials.

The scapula, with its distinctively tapiroid notch in the anterior border, is intermediate in contour between the cursorial and graviportal digitigrade types.

The fore-limb mediportal characters of *Tapirus* are (*a*) rounded rather than angulate superior border of scapula; (*b*) prominent tuber spinae of the scapula; (*c*) no acromion scapulae; (*d*) prominent great tuberosities of the humerus. A primitive mediportal character of the humerus is the equal development of the muscular attachments on the inner and outer sides of the distal ends of the humerus, as reflected in entocondyle and ectocondyle of equal size. A primitive character of both *Tapirus* and *Heptodon* is the asymmetry of the distal rotula and capitellum of the humerus.

Throughout all its parts the species *T. terrestris* is slightly more cursorial in type than *T. indicus*. This difference is observed in both the fore and hind limbs; the olecranon of the ulna alone exhibits a marked difference of character.

The hind limb of *Tapirus* is of the primitive mediportal type. The femur is somewhat longer than the tibia, the great trochanter is prominent, the second and third trochanters are less elevated on the shaft than in *Heptodon*. As in the fore limb, *T. indicus* is seen to be more graviportal than *T. terrestris*, especially in the weight of the shaft of the femur and prominence of the great trochanter.

THE LOPHIODONTS

Heptodon is to be regarded as a precociously cursorial lower Eocene relative of the heavy-bodied Lophiodontidae of Europe. Its radius equals the humerus in length and the tibia equals the femur, whereas in *Tapirus* the corresponding proportions are the reverse, the humerus exceeding the radius, the femur exceeding the tibia. This is the primitive mediportal condition. The radius and ulna are relatively elongate, and the olecranon of the ulna is erect. The tuberosity of humerus is moderately developed. A primitive character of *Heptodon* is the persistent acromial rugosity of the spine of the scapula.

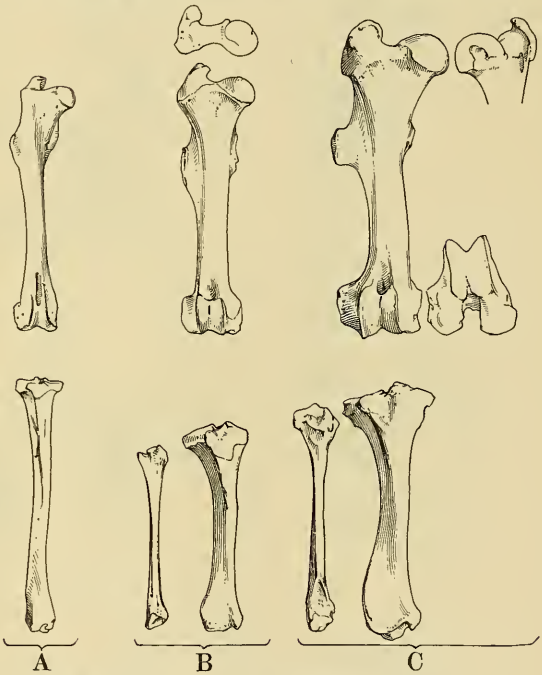


FIGURE 676.—Limb structure of perissodactyls: Hind limbs of *Heptodon* and *Tapirus*

A, *Heptodon calciculus* (family Lophiodontidae), one-fourth natural size; B, *Tapirus terrestris*, and C, *Tapirus indicus* (family Tapiridae), one-sixth natural size. Showing the contrast between a primitive cursorial type (*Heptodon*) and a persistent mediportal type (*Tapirus*).

The cursorial characters of the hind limb of *Heptodon* are seen in the elongate tibia and the elevation of the second and third trochanters on shaft.

PALAEOTHERIIDAE

The adaptive radiation of the paleotheres (*Palaeotherium, Paloplotherium*) into animals of greater or less speed and weight was observed by Cuvier. The bones of the fore limb, here figured after De Blainville

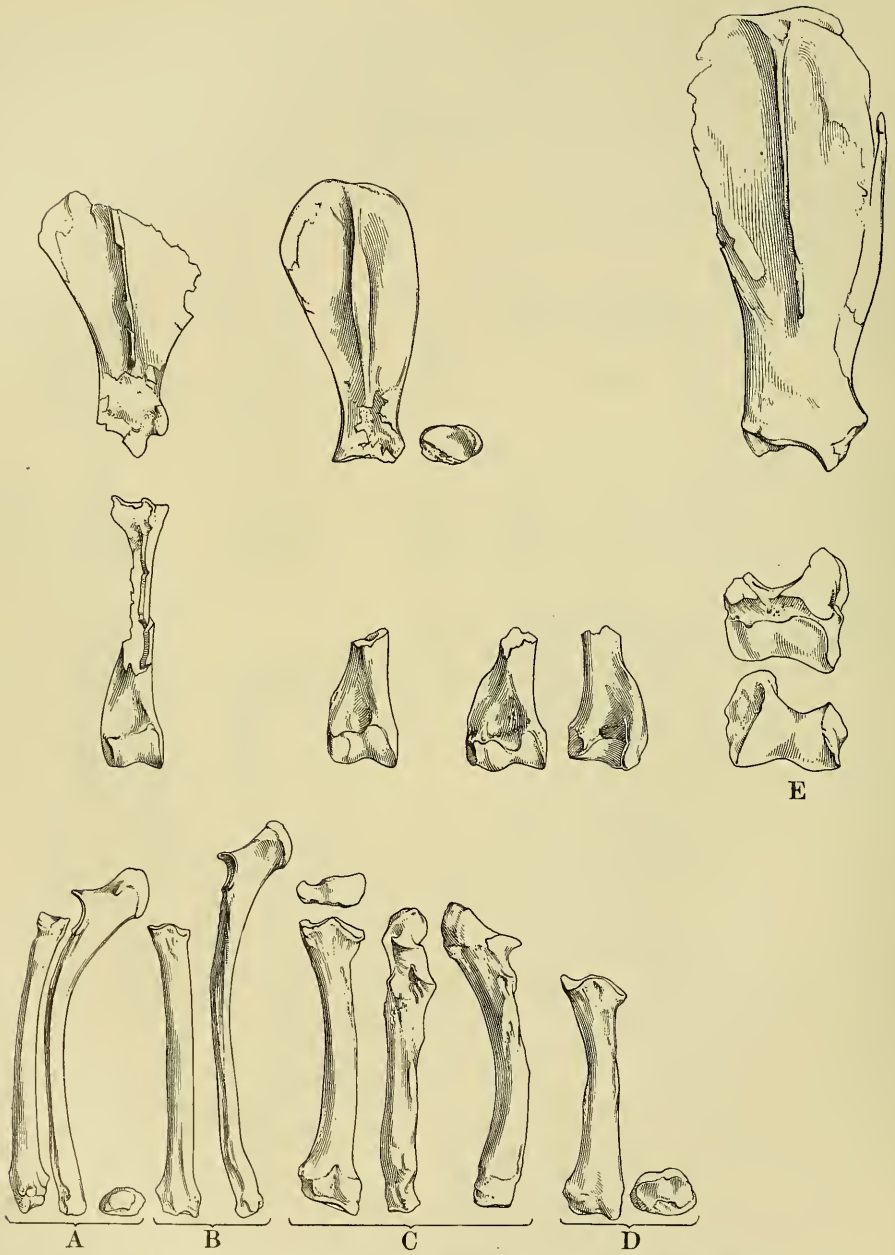


FIGURE 677.—Limb structure of perissodactyls: Fore limbs of paleotheres

Arch and limb segments showing contrasts. A, *Palaeotherium medium* (subcursorial); B, *Palaeotherium* sp., and C, *P. crassum* (mediportal); D, *P. latum*, and E, *P. magnum* (subgraviportal). After De Blainville, 1839.1. One-fourth natural size.

(1839.1, pls., vol. 4, *Palaeotherium*, pls. iii and iv), are too incomplete to afford allometric ratios, but they conform strictly to the universal principles of speed and weight allometry. The elongate radius of *Paloplotherium minus* parallels that of the lightest cursorial types of Equidae. In *Palaeotherium medium* the radius exceeds the humerus in length, a subcursorial ratio. Weight-bearing progression from *P. medium* to *P. crassum* and *P. latum* is indicated in the broadening of the collum scapulae and shortening of the radius.

The fan-shaped scapula of *Palaeotherium medium* parallels that of the earlier cursorial horses like *Mesohippus;* the ovate-shaped scapula of *P. crassum* parallels that of the mediportal rhinoceroses like *R.* (*Dicerorhinus*) *sumatrensis;* the elongate scapula of *P. magnum* parallels that of the graviportal (black rhinoceros) type, namely, *R.* (*Opsiceros*) *bicornis.*

In the hind limb, similarly, the tibia of *Palaeotherium medium* apparently exceeds in length the femur and presents a "subcursorial" ratio. In the femur of *P. latum*, *P. crassum*, and *P. magnum* the third trochanter is very low down on the shaft, as in graviportal forms; this is paralleled in the modern graviportal rhinoceroses such as *R.* (*Dicerorhinus*) *sumatrensis.* The knee is strongly flexed, the patellar facet being very oblique with reference to the shaft of the femur, as in early amynodonts and rhinoceroses.

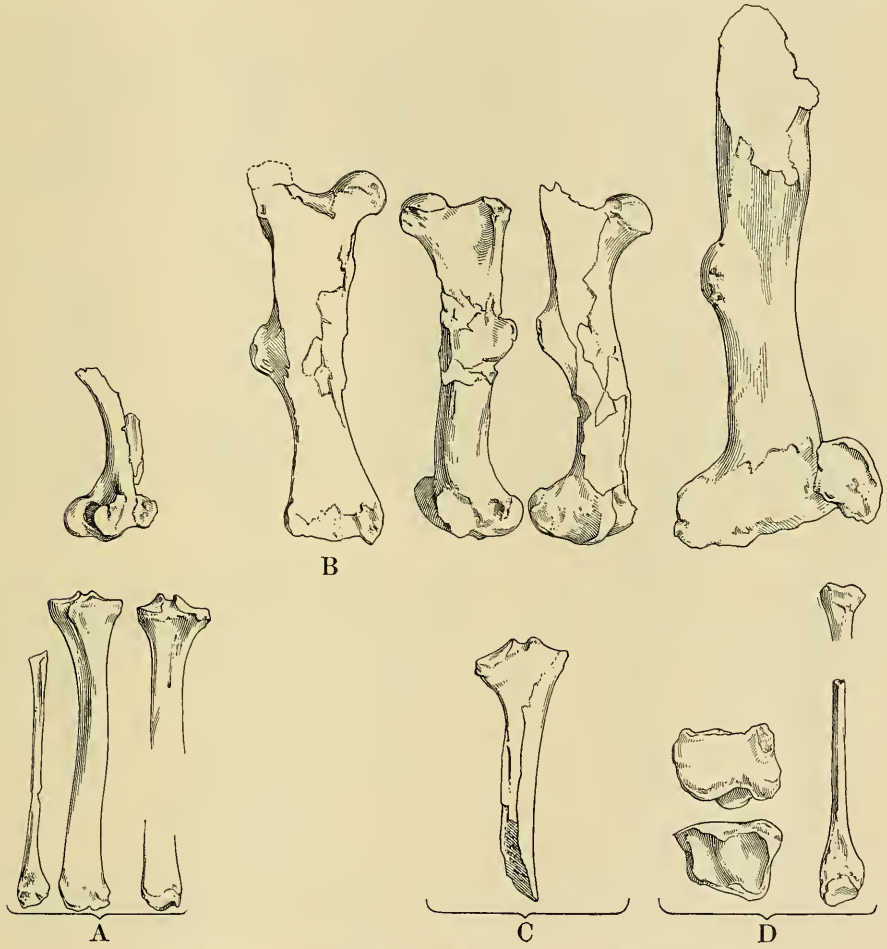


FIGURE 678.—Limb structure of perissodactyls: Hind limbs of paleotheres

Limb segments showing contrasts. A, *Palaeotherium medium* (subcursorial); B, *P. latum;* and C, *P. crassum* (mediportal); D, *P. magnum* (subgraviportal). After De Blainville, 1839.1. One-fourth natural size.

RHINOCEROTIDAE, HYRACODONTIDAE, AMYNODONTIDAE

The extensive series of rhinoceros limb segments shown in Figure 679 illustrates all the principles of contrasting speed and weight progression. These animals have no genetic relationship; they belong to four entirely distinct subfamilies. The following points appear: (1) It is noteworthy that the Eocene rhinocerotoid types (*Triplopus*, *Hyrachyus*, *Hyracodon*) and even the Oligocene forms (*Caenopus*) are either subcursorial or cursorial. (2) A syngenetic resemblance between all the rhinoceroses is seen in the abbreviated spine of the scapula and in the elevated position of the tuber spinae. (3) The scapulae represent four adaptive types, namely, the elongate cursorial (*Hyrachyus*), the mediportal (*Caenopus*), the lobate or vertically elongate graviportal-digitigrade (*Rhinoceros* (*Opsiceros*) *bicornis*), and the triradiate graviportal (*Metamynodon*, *Teleoceras*). (4) Contrasting the limbs of *Triplopus* and *Metamynodon*, we observe the two extremes of cursorial and graviportal allometry.

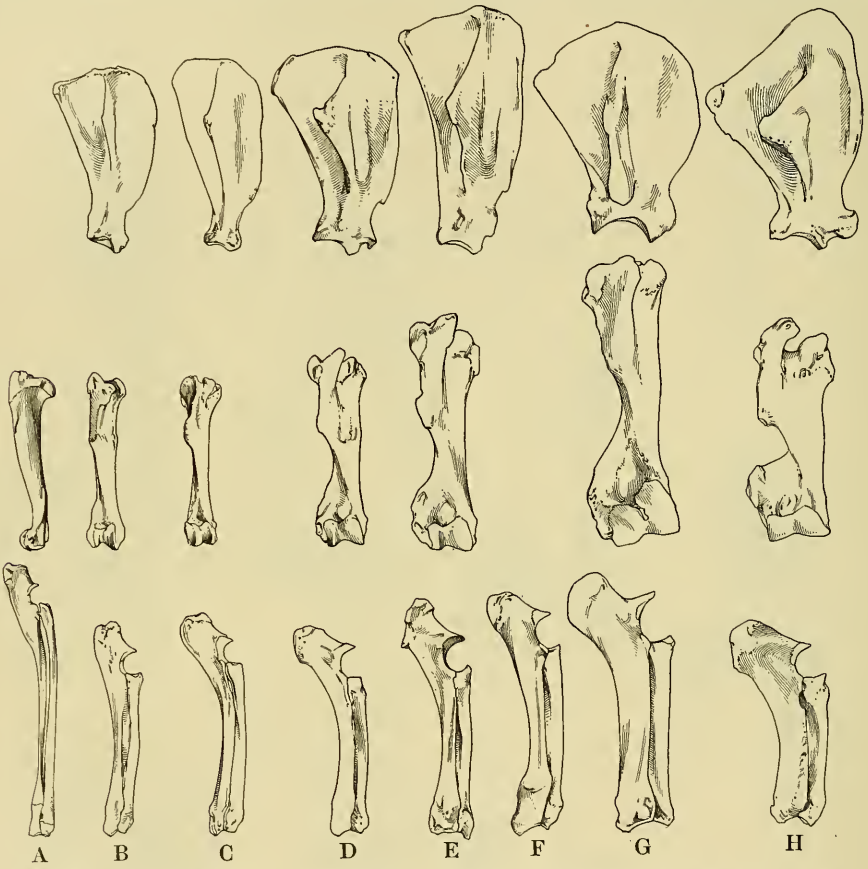


FIGURE 679.—Limb structure of perissodactyls: Fore limbs in four American rhinoceros subfamilies

Limb segments of (A) *Triplopus cubitalis*, (B) *Hyrachyus agrarius*, (C) *Hyracodan nebrascensis*, (D) *Caenopus accidentalis*, (E) *Caenopus tridactylus*, (F) *Amynodan intermedius*, (G) *Metamynodon planifrons*, and (H) *Teleoceras fossiger*, showing the contrasts between subcursorial types (*Hyrachyus*, *Hyracodon*, family Hyracodontidae), a mediportal type (*Caenopus*), and graviportal types (*Metamynodan*, family Amynodontidae; *Teleoceras*, subfamily Teleoceriinae). A, about two-sevenths natural size; B, C, about one-seventh natural size; D–H, about one- ninth natural size.

We first observe a very pronounced difference between the trihedral graviportal scapulae of *Metamynodon* and *Teleoceras* and the elongate lobate scapula of all the Old World modern rhinoceroses.

The graviportal progression, as illustrated in these rhinoceroses, advances through the following changes: (1) The scapulohumeral ratio decreases in the graviportal American rhinoceroses (*Metamynodon*, *Teleo-*

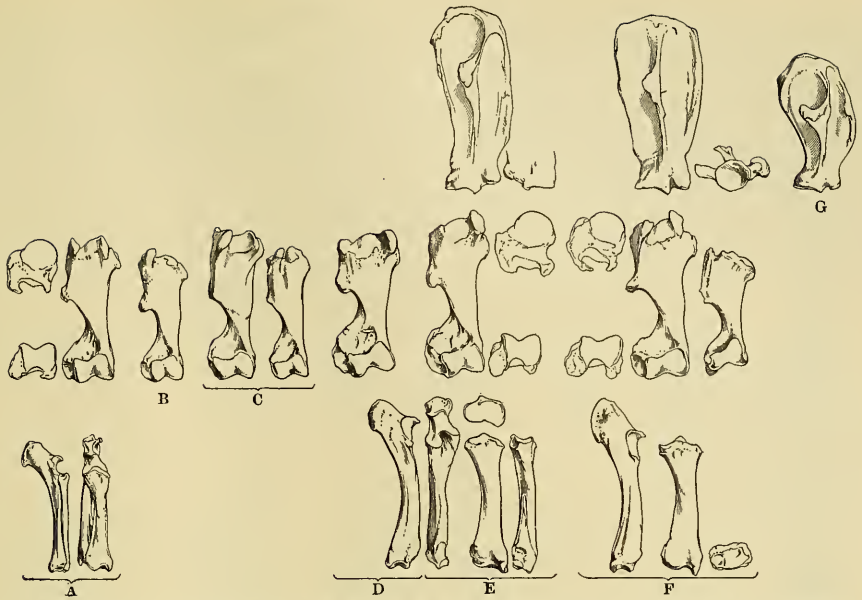


FIGURE 680.—Limb structure of perissodactyls: Fore limbs in four Old World rhinoceros subfamilies

Aceratheriinae, Ceratorhinae (Sumatran), Rhinocerotinae (Indian), and Dicerotinae (African), represented by (A) *Ceratorhinus sumatrensis*, (B) *C. leptorhinus*, (C) *Aceratherium incisivum*, (D) *Ceratotherium simum*, (E) *Opsiceros* (*Diceros*) *bicornis*, (F) *Rhinoceros indicus*, (G) *R. javanicus*. Somewhat less than one-tenth natural size.

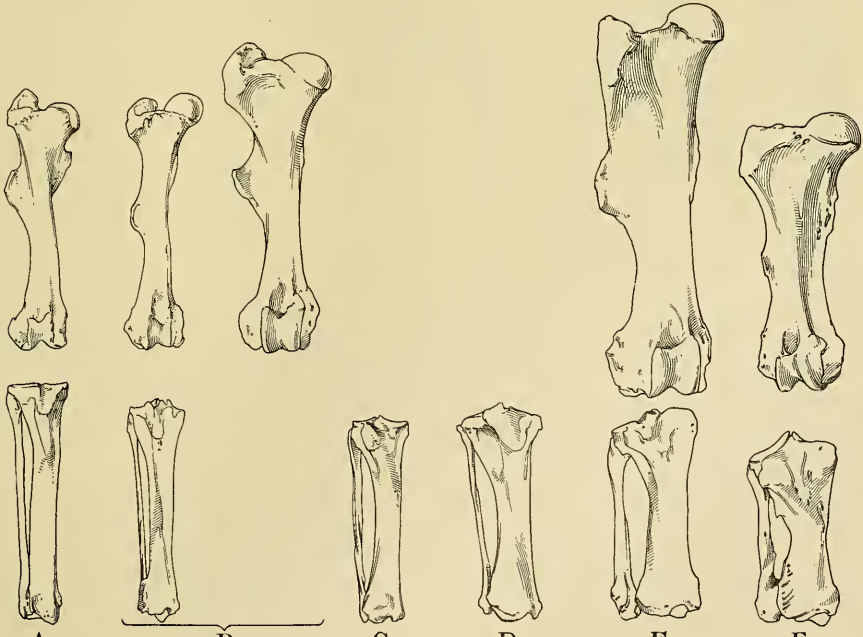


FIGURE 681.—Limb structure of perissodactyls: Hind limbs of rhinoceroses found in North America

A, *Hyrachyus agrarius;* B, *Hyracodon nebrascensis;* both one-sixth natural size. C, *Caenopus occidentalis;* D, *Amynodon intermedius;* E, *Metamynodon planifrons;* F, *Teleoceras fossiger;* all one-eighth natural size. These represent the four subfamilies of Hyracodontinae, Aceratheriinae, Amynodontinae, and Teleocerinae.

ceras), in which the scapula shortens and the humerus elongates; not so in the Old World rhinoceroses (*R.* (*Opsiceros*) *bicornis, R. unicornis*), in which the scapula exceeds the humerus in length; (2) the humeroradial ratio increases in *Teleoceras* and *Metamynodon* only—that is, the radiohumeral ratio decreases; (3) in the Old World rhinoceroses the radius remains relatively of the same length as the humerus; (4) the neck ("collum") of the scapula broadens; (5) the posterosuperior border of the scapula becomes depressed (American graviportal genera only); (6) the infraspinous fossa of the scapula increases (*Metamynodon, Teleoceras*); (7) the supra- and infraspinous fossae are equal or balanced in the heavy Old World types (*Rhinoceros, Opsiceros*); (8) the tuber spinae of the scapula increases and points upward; (9) the great tuberosity of the humerus rises above the head; (10) the deltoid crest is lowered to the middle of the shaft and rises in prominent tuberosities; (11) the ectocondylar crest of the humerus rises on the shaft, the entocondylar crest disappears; (12) the ulna olecranon becomes recumbent and expanded distally.

This series parallels the progression characteristic of graviportal titanotheres in certain features but not in others.

This series represents a sequence of adaptive types but not a phylogenetic sequence. It includes members of four subfamily types, namely, hyracodont (subcursorial), aceratheriine (mediportal), amynodont (graviportal-digitigrade), and rhinocerotine (graviportal-digitigrade). The comparison between the cursorial, mediportal, and graviportal limbs exhibits the following laws of progression from subcursorial and mediportal to graviportal adaptation: First the tibia relatively shortens, thus the femorotibial ratio increases, or the tibiofemoral ratio decreases; the shaft of the femur broadens, flattens, and straightens (*Amynodon, Teleoceras, Rhinoceros, Opsiceros*); the great trochanter, which is narrow and elevated in cursorial hyracodonts, becomes broad and depressed in the graviportal amynodonts, in *Teleoceras*, and in *Rhinoceros;* the third trochanter shifts from above downward to the middle part of the shaft and becomes very prominent (the rhinoceroses are unique in this

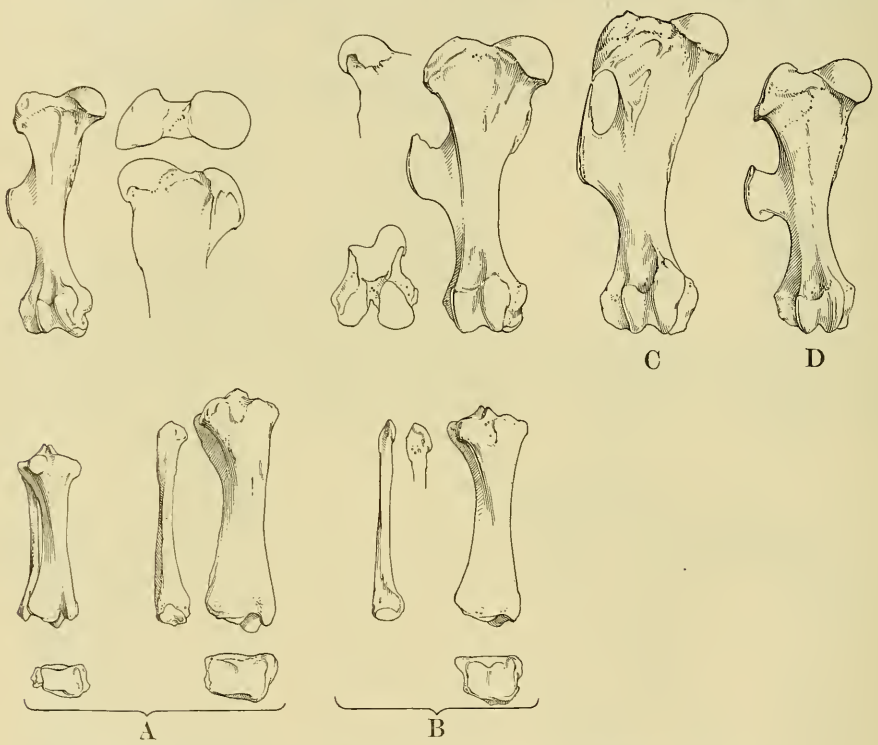


FIGURE 682.—Limb structure of perissodactyls: Hind limbs of rhinoceroses found in the Old World

A, *Ceratorhinus sumatrensis;* B, *Opsiceros* (*Diceros*) *bicornis;* C, *Rhinaceros indicus;* D, *R. javanicus.* One-tenth natural size.

character); the second trochanter remains on the upper part of the shaft and becomes less prominent; the femoropatellar facet becomes more anterior (*Metamynodon*) as the limb straightens out; the patellar facet rises on the front of the shaft of the femur as the knee becomes less flexed and the hind limb more vertical; the same facet becomes more asymmetrical (a progressive syngenetic but not distinctively a graviportal character).

which show signs of adaptation to increased weight. The cursorial maximum is reached in the lower Pliocene *Hipparion* (*Neohipparion*), after which there is a retrogression to the more heavy-bodied *Equus* and *Hippidium*.

It is striking to observe how early in geologic time certain cursorial characters are attained in the horse

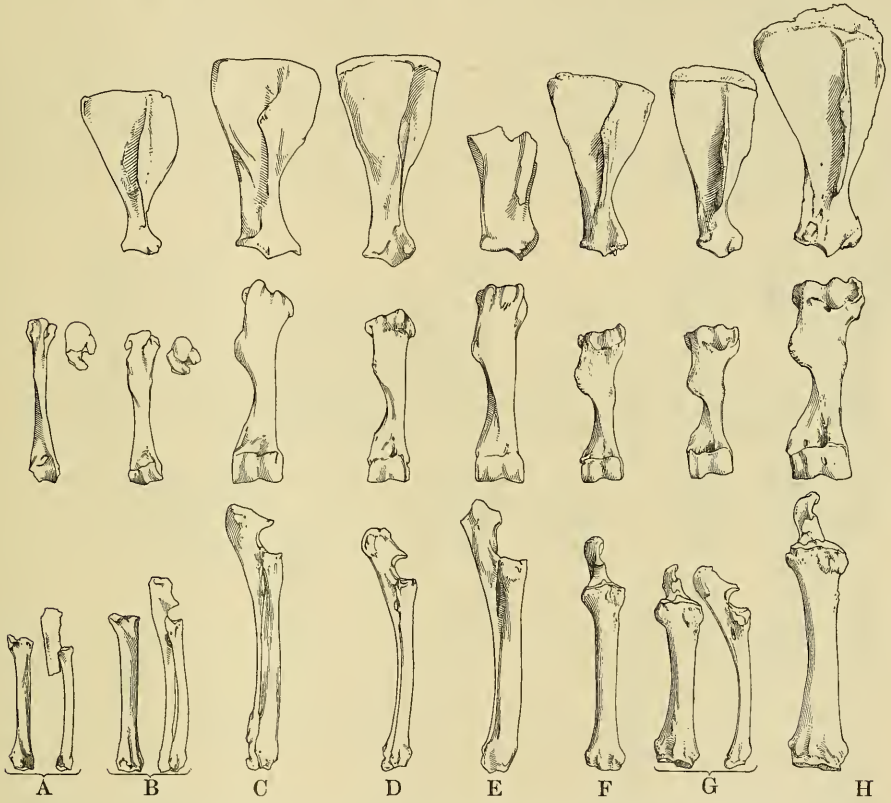


FIGURE 683.—Limb structure of perissodactyls: Fore limbs of Equidae, showing their cursorial adaptation

A, *Orohippus osbornianus*, two-sevenths natural size. B, *Mesohippus bairdi*, one-fifth natural size. C, *Hypohippus osborni;* D, *Neohipparion whitneyi;* E, *Hipparion gracile;* all one-seventh natural size. F, *Equus kiang;* G, *Equus burchelli;* H, *Equus caballus;* all one-ninth natural size. Scales approximate. After De Blainville, 1839.1, and Osborn.

EQUIDAE

The accompanying figures (683, 684) represent individuals selected from polyphyletic series of Equidae beginning with the primitive Eocene cursorial and light-bodied types, including the Oligocene cursorials and the extremely cursorial *Neohipparion*, the Pliocene *Hipparion*, and the modern heavy-bodied *Equus*, family. Among the fore limb cursorial adaptations of Eocene equines are (1) scapula with relatively small supraspinous fossa (as in cursorial Artiodactyla); (2) with narrow "collum scapulae"; (3) with fan-shaped blade; (4) ulna with elongate vertical olecranon. A persistent primitive character is the acromial rugosity of the spine of the scapula.

Additional cursorial adaptations acquired after Eocene time are (1) reduction of tuber spinae scapulae; (2) scapulohumeral ratio increase; (3) humero-

radial ratio decrease; (4) radiohumeral ratio increase; (5) metacarpohumeral ratio increase; (6) tuberosities of humerus become less elevated or prominent, whereas they become more prominent in graviportal digitigrades; (7) entocondylar crest of humerus reduced, ectocondylar crest slightly expanded; (8) spine of scapula abbreviated.

The speed ratios and speed contours are progressively acquired up to and including *Neohipparion*, the most light-limbed horse known. The retrogression of these speed ratios through *Equus asinus* and *E. caballus* and into the very slow-moving *Hippidium* is due to the increasing weight of these animals. In this graviportal retrogression (1) the olecranon of the ulna becomes more robust and recumbent; (2) the neck of the scapula broadens; (3) the deltoid and ectocondylar crests become more prominent.

BRONTOTHERIIDAE—THE TITANOTHERES

The adaptive progression from left to right, as shown in the accompanying diagrams (figs. 685, 686), is from subcursorial (*Eotitanops*) through mediportal (*Mesatirhinus*) to graviportal (*Brontotherium*) types. In the scapula *Palaeosyops*, a heavy type, shows incipient trihedral form; *Brontops* becomes markedly trihedral with prominent tuber spinae.

Adaptation to graviportal progression in the fore limb is as follows: (1) Elevation of the great tuberosity of the humerus into a broad plate, (2) lowering on the shaft and great prominence of deltoid crest, (3) production of deltoid tuberosity, (4) elevation of ectocondylar crest, (5) obliquity and asymmetry of humeroradial trochlea, (6) depression and thickening of olecranon of ulna.

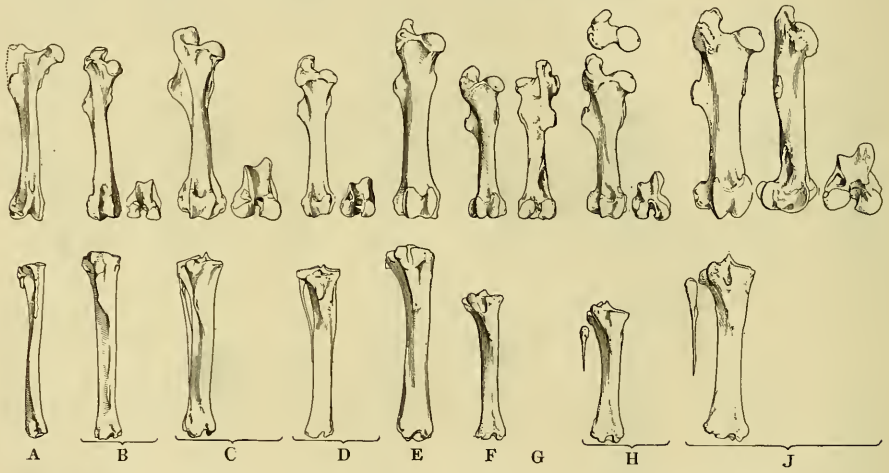


FIGURE 684.—Limb structure of perissodactyls: Hind limbs of Equidae, showing their cursorial adaptation

A, *Orohippus osbornianus*, one-fourth natural size. B, *Mesohippus bairdi*, one-fifth natural size. C, *Hypohippus osborni*; D, *Neohipparion whitneyi*; E, *Hipparion gracile*; C–E one-seventh natural size. F, *Equus kiang*; G, *Equus asinus*; H, *Equus burchelli*; J, *Equus caballus*; F–J one-ninth natural size. Scales approximate. After De Blainville, 1839.1, and Osborn.

A distinctive and syngenetic character of the Equidae is the doubling of the bicipital groove by the development of a median convexity. The degeneration of the ulna and fibula inferiorly is a special equine and also a general cursorial character (ulna reduced and fibula disappears in cursorial ruminants).

In the hind limb the chief cursorial progression is as follows: (1) Femorotibial ratio decreases; (2) tibiofemoral ratio increases; (3) third trochanter rises on shaft; (4) second trochanter relatively decreases in prominence. The increasing asymmetry of the femoropatellar facets may not be regarded as a distinctively cursorial progressive character because it is also observed in the graviportal rhinoceroses.

The platelike form of the great tuberosity of the humerus is a distinctive titanothere character. Another distinctive feature is that in the titanotheres the radius increases in length as compared with the humerus, whereas in graviportal rhinoceroses the radius either remains of the same length or abbreviates (*Metamynodon, Teleoceras*).

A relatively straight or vertical hind limb, with little flexure of the knee joint, anterior patellar facet, and relatively short (graviportal) tibia, appears to have characterized the titanotheres from the middle Eocene onward. The graviportal progression, as seen in Figure 686, results in the following changes: (1) Reduction in size of the crest of the great trochanter (rather

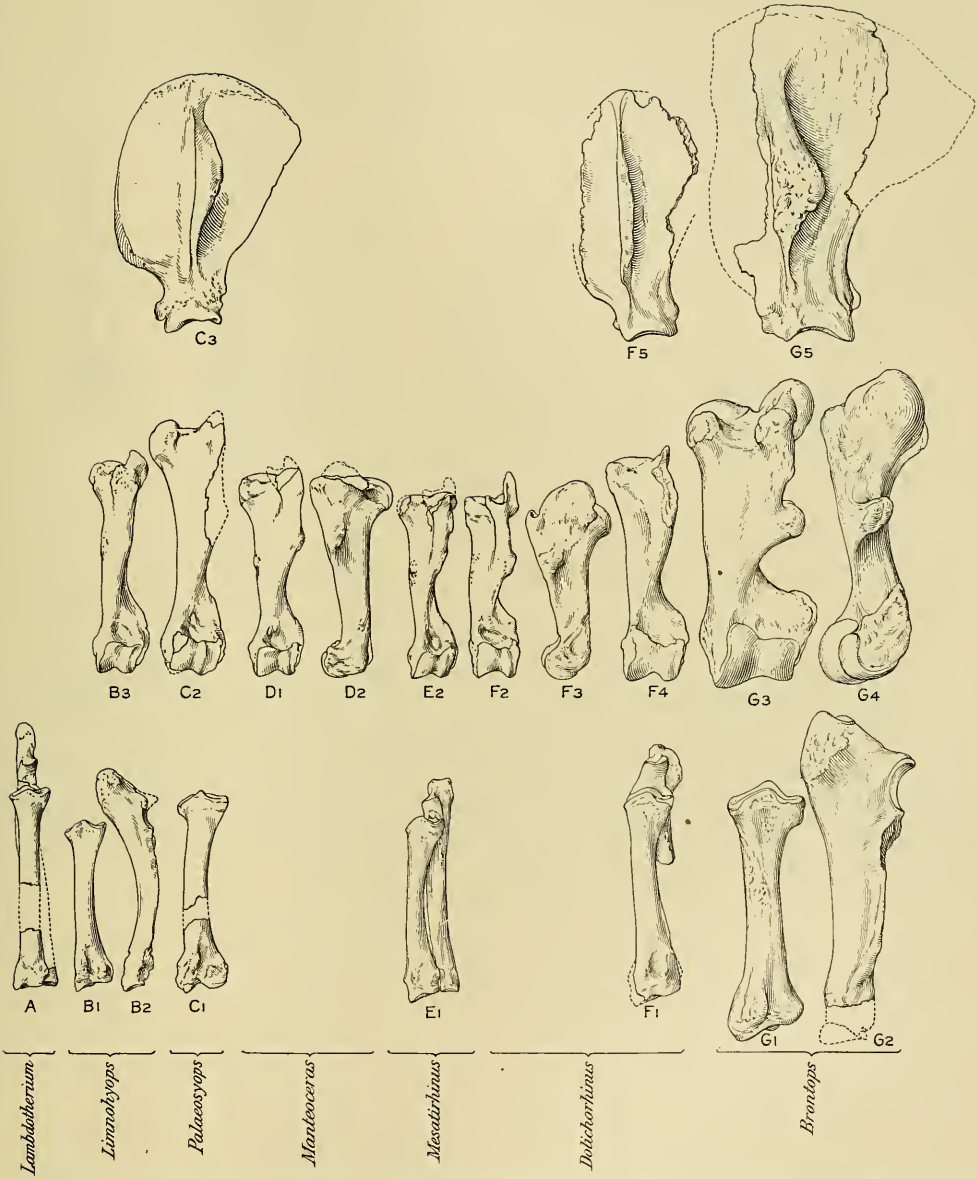


FIGURE 685.—Limb structure of perissodactyls: Fore limbs of Eocene and Oligocene titanotheres belonging to several phyla

These limb segments (proximal elements above, distal below) show the range of adaptation, which includes subcursorial (A), mediportal (B–F), and graviportal (G) types. A, *Lambdotherium*, one-third natural size. B_1–B_3, *Limnohyops*; C_1–C_3, *Palaeosyops*; D_1, D_2, *Manteoceras*; E_1, E_2, *Mesatirhinus*; F_1–F_5, *Dolichorhinus*; B–F one-eighth natural size. G_1–G_5, *Brontops*, one-twelfth natural size. Scales approximate.

than its depression as seen in other graviportal types); (2) lowering of the lateral rugosity of the great trochanter to unite with that of the third trochanter; (3) depression and lowering of the third trochanter from the upper to the middle portion of the shaft (paralleling *Astrapotherium* and differing from the typical rectigrades, such as *Mastodon*, in which the second and third trochanters become sessile); (4) lowering of the second trochanter toward the middle portion of the shaft (thus differing from other graviportal digitigrades, such as *Rhinoceros*, in which the second trochanter remains high up on the shaft); (5) great elongation of the femur and abbreviation of the tibia, noteworthy in *Manteoceras* and extreme in *Brontotherium;* (6) straightening, flattening, and elongation of the shaft of the femur to parallel the graviportal rectigrade type (*Elephas*) far more closely than the graviportal digitigrade type of the rhinoceroses. Both the syngenetic and teleogenetic characters of the femur are seen to be quite distinct from those of other graviportal perissodactyls and are very distinctive throughout the series. The only analogy with members of other families is seen in the comparison of the hind limb of *Mesatirhinus* and *Tapirus terrestris*, but this is not very close.

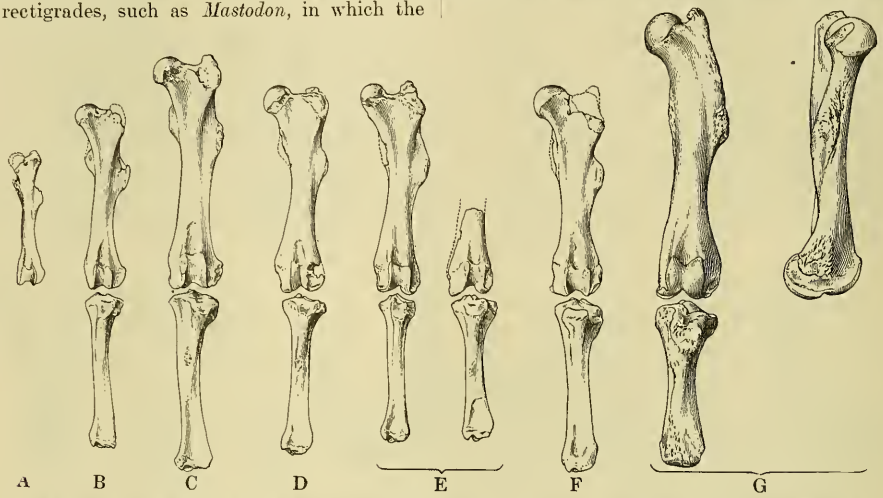


FIGURE 686.—Limb structure of perissodactyls: Hind limbs of Eocene and Oligocene titanotheres belonging to several phyla

These limb segments (proximal elements above, distal below) show the range of adaptation, which includes subcursorial or primitive mediportal (A), mediportal (B–F), and graviportal (G) types. A, *Eotitanops princeps;* B, *Mesotirhinus petersoni;* C, *Palaeosyops major;* D, *Limnohyops monoconus;* E, *Manteoceros manteoceras;* F, *Dolichorhinus hyognathus;* G, *Brontops robustus.* A–F, one-ninth natural size; G, one-fourteenth natural size. Scales approximate.

CHAPTER X

THEORIES AS TO THE ORIGIN, ANCESTRY, AND ADAPTIVE RADIATION OF THE TITANOTHERES AND OTHER ODD-TOED UNGULATES

SECTION 1. ORIGIN AND RELATIONSHIPS OF THE PERISSODACTYLA

NATURE AND HABITAT OF THE ANCESTRAL PERISSODACTYL

As shown in Chapter I, the branching off of the titanotheres from the other lower Eocene perissodactyl families—the horses, tapirs, and lophiodonts—points to the very great antiquity of the titanothere stock, to basal Eocene or closing Cretaceous time, when there probably existed a stem perissodactyl, doubtless a very small animal. This little quadruped was probably an inhabitant of the plateau regions of Asia, from which its descendants diverged through adaptive radiation into the ancestral nine great perissodactyl families that entered Europe and North America. It is certain that this adaptive radiation took place long before the beginning of Eocene time, for there is evidence that at the beginning of the Eocene epoch at least five of these perissodactyl families had acquired their distinctive family characters, especially those of the teeth.

The grounds on which are based the theory of the derivation of the perissodactyls from a single perissodactyl stem are twofold. First, the members of each of the families preserve certain persistent primitive (paleotelic) ancestral characters, inherited in common from the perissodactyl stem form; second, each of these families exhibits in common certain potentialities (cenotelic) of evolutionary development, expressed in the progressive or advancing characters that each exhibits.

This twofold affinity displayed in similar ancestral character and in similar progressive characters is a dominant feature in classification, which has been exemplified repeatedly in the preparation of this monograph. It is now seen to apply to orders as well as to families, genera, and species.

The common characters of members of the perissodactyl families are listed below.

Persistent primitive ancestral characters

1. A complete series of upper and lower incisor and canine teeth, as in all primitive Ungulata, Condylarthra, and Amblypoda.
2. Upper and lower grinding teeth originally with six rounded, conical cusps, as in the Condylarthra and Artiodactyla, but differing from those of the Amblypoda.
3. Base of the skull with an alisphenoid canal for the transmission of the external carotid artery, as in Condylarthra and many Creodonta; reduced or absent in Artiodactyla.
4. Dorsal and lumbar vertebrae 20 or 21, as compared with Condylarthra, which have 19–20, and Artiodactyla, which have 20.
5. Femur with a third trochanter, as in Condylarthra; reduced or absent in Artiodactyla.
6. Manus with only four digits; pollex absent or much reduced; five digits in Condylarthra; five digits in primitive Artiodactyla.
7. Pes with distinctive perissodactyl ankle joint, quite distinct from that of Condylarthra or Artiodactyla.

Potential new progressive characters

8. Premolars tending to transform into the molar pattern, a very rare character in Artiodactyla.
9. Manus originally mesaxonic, secondarily paraxonic; in the Artiodactyla originally and persistently paraxonic.
10. Tarsus losing the ancestral middle ankle joint by flattening the articulation between the astragalus and the navicular; perfecting the tibiotarsal joint by mechanical play between tibia and astragalus.
11. Fibula gradually losing its calcaneal facet; fibulocalcaneal facet persistent and specialized in Artiodactyla.
12. Progressive specialization and adaptive radiation of the brain, skull, teeth, trunk, limbs, and feet for a great variety of habits and habitats in the nine different families.

The characters indicated in this list debar the Perissodactyla from community of descent with the Artiodactyla (see Gregory, 1910.1, pp. 385–386), as was believed by Cope when he proposed the superorder Diplarthra to include the perissodactyl and artiodactyl stems. In the opinion of Osborn they also debar the Perissodactyla from descent from the Condylarthra, typified by *Phenacodus* of the lower Eocene and *Euprotogonia* of the basal Eocene, as believed by Cope in regarding the perissodactyl order as an offshoot from the Condylarthra. Structurally, as Gregory has shown (op. cit., pp. 387–397), the ancestral perissodactyl resembled certain more primitive condylarths (*Euprotogonia*) in many features, although it differed from them fundamentally in the ankle joint; but in their potentiality of progressive evolution in the characters shown in Nos. 8 to 12 above, the momentum of the Perissodactyla can not be derived from the inertia of the Condylarthra. We thus can not agree with Gregory (op. cit., p. 397) that "the derivation of the perissodactyl order from the general insectivore-creodont-condylarth group of placentals seems fairly well established." It appears more probable that the perissodactyls sprang from some entirely unknown progressive placental source—large-brained, plastic—to which Osborn has given the name Ceneutheria, as distinguished from the archaic non-

progressive Meseutheria, which includes the Amblypoda and Condylarthra, theoretical branches of relatively archaic and conservative stock (see Gregory, 1910.1, p. 458). This question is, however, still an open one and is of so much importance and interest in connection with the whole problem of the evolution of the hoofed mammals that it is desirable to review it in more detail in the light of our present knowledge. The final solution must await the discovery, probably in Asia, of the actual Upper Cretaceous and basal Eocene ancestors of the perissodactyls.

CARPUS OF CREODONTA, AMBLYPODA, CONDYLARTHRA

Our present (1918) knowledge of the structure of the carpus in these primitive orders of mammals is displayed in the accompanying Figure 687. All are pentadactyl, possessing five more or less spreading digits. The creodont *Dissacus*, the amblypod *Pantolambda*, and the primitive condylarths *Euprotogonia* and *Meniscotherium* are more or less plantigrade. The condylarth *Phenacodus* is secondarily digitigrade and tending toward tridactylism.

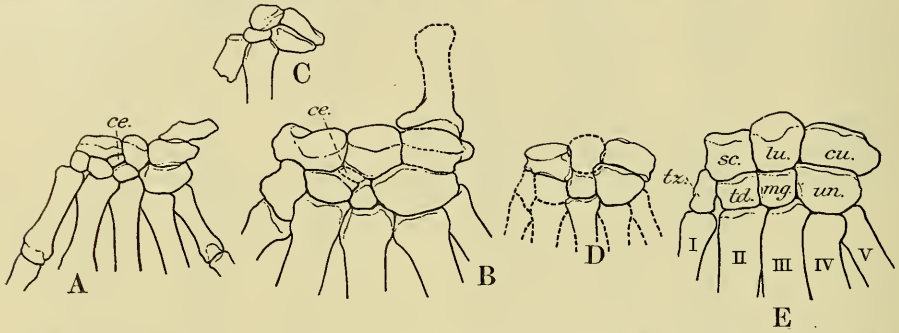


FIGURE 687.—Carpus of Creodonta, Amblypoda, and Condylarthra, showing the primitive "alternating" placental type and the specialized "serial" type

Pentadactyl

Creodonta:

A, *Dissacus carnifex*. Four-ninths natural size. A primitive placental type. Magnum small, supporting centrale and half of lunar; lunar wedge-shaped, resting on magnum and unciform.

Amblypoda:

B, *Pantolambda bathmodon*, Am. Mus. 2547. Natural size. Magnum small, supporting centrale and part of lunar; lunar wedge-shaped, resting on magnum and unciform.

Condylarthra:

C, *Meniscotherium* sp. Natural size. Magnum small, supporting centrale and lunar; lunar flattened, resting on magnum and unciform.

D, *Euprotogonia*. Four-thirds natural size. Magnum small, truncate, partly supporting scaphocentrale; chiefly supporting lunar; lunar truncate, retaining contact with unciform.

Mesaxonic

E, *Phenacodus*. Two-thirds natural size. Serial type. Magnum enlarged, truncate, wholly supporting lunar; lunar truncate, resting chiefly on magnum, with small contact with unciform.

HYPOTHETICAL ORIGIN OF THE PERISSODACTYLA FROM THE CONDYLARTHRA

HISTORY OF OPINION

Cope (1884–1898) regarded the Condylarthra, typified by *Euprotogonia* and *Phenacodus*, as representives of the long sought five-toed ancestors of the perissodactyls. Osborn (1890.51) at first accepted this view and with Cope regarded the manus of *Phenacodus* as close to the primitive foot of the Perissodactyla and Ungulata; but in 1893 (1893.82, p. 89) he abandoned Cope's view and proposed the theory that the Condylarthra were part of an archaic ungulate radiation not directly ancestral to the perissodactyls. Subsequently Osborn developed the idea (1894.89) that the source of the Perissodactyla was to be sought far back of the Condylarthra.

The serial carpus of *Phenacodus*, as first observed by Matthew, is obviously secondary when compared with that of *Euprotogonia*. This important fact compels us to abandon Cope's great hypothesis that the serial or taxeopod type was ancestral to that of all the Ungulata; certainly the Amblypoda and Condylarthra did not spring from a "serial" type.

This fact also modifies many of the conclusions which Osborn reached in his "Evolution of the ungulate foot" (1890.51, p. 531), a treatise based upon the adoption of Cope's theory that the common protungulate foot was serial.

Matthew (1897.2, pp. 309–310) showed that the taxeopod, serial foot of *Phenacodus* is not primitive but secondary, because the foot of its ancestor *Euprotogonia* has partly alternating or displaced carpals. He reached the following conclusion (op. cit., pp. 300, 308, 309):

While we are unable to consider *Euprotogonia* the direct ancestor of the Perissodactyla, yet it had many characters approximating it to them. It is probable that the common ancestor of the typical Ungulata was thoroughly an unguiculate and that the first separation into the phyla of phenacodonts, perissodactyls, and artiodactyls accompanied or preceded the development of hoofs from claws [p. 300]. * * * This evidence, though not conclusive, points unmistakably toward an alternating carpus as the primitive one. In *Phenacodus* the carpus is more nearly serial, although it varies in different individuals, and there is always a lunar-unciform contact. But if *Phenacodus* is a direct descendant of *Euprotogonia* this serialism must be secondary [pp. 308, 309]. We must go somewhat lower down than the Torrejon [that is, Thanetian] to find the junction of the equine and phenacodont phyla.

Osborn (1898.148, p. 174) accepted Matthew's conclusion and agreed that the primitive ungulate foot was interlocking, or alternating (lunar on unciform, scaphocentrale on magnum), derivable from that of such a creodont type as *Dissacus*, from which the carpus of the Amblypoda and Condylarthra and possibly of all Ungulata may be derived.

Gregory (1910.1, p. 385) observes:

The question of the derivation of the perissodactyls as an order and of their relationship to the Condylarthra is still open. Cope saw in *Phenacodus* the atavus of practically all the hoofed orders. Osborn holds the contrary opinion that *Phenacodus* is a hoofed offshoot of the Creodonta and a member of the Meseutheria, or small-brained Cretaceous-basal Eocene orders, and that the perissodactyls have sprung from some entirely unknown "Caeneutheria" (p. 457). * * * Still another view may be adduced—that although neither *Phenacodus* nor *Euprotogonia* were the ancestors of the Perissodactyla yet they resemble those forms more nearly than do any other known mammals; and that the basal Eocene ancestors of the Perissodactyla would, if discovered, fall under the superorder Protungulata as defined above (p. 383).

The Protungulata are then defined as typified by the condylarth *Euprotogonia*. Gregory reaches the conclusion (op. cit., p. 396) that

The ancestral perissodactyl as thus conceived resembled the more primitive condylarths such as *Euprotogonia* in many features (p. 397). * * * To conclude, the derivation of the perissodactyl order from the general insectivore-creodont-condylarth group of placentals seems fairly well established. * * * On the other hand, genetic derivation from any well-known condylarths (*Phenacodus*, *Euprotogonia*, *Meniscotherium*) is almost equally improbable. But with regard to many important dental and osteological features it is obvious also that *Euprotogonia* and *Phenacodus* bridge over the structural gap between the perissodactyls and the lower unguiculate orders and, in brief, that the stem of the perissodactyls would very likely fall under the Condylarthra, as redefined by Matthew (1897).

After summing up all the characters of the stem perissodactyls and comparing them in detail with the characters of *Euprotogonia* Gregory concludes (op. cit., p. 389):

It is not denied that the ancestral perissodactyl had a larger brain case and better brain than *Euprotogonia*. It is merely inferred that there was a considerable variation in brain charac-

FIGURE 688.—Evolution of the upper molar pattern in condylarths and titanotheres

In the earliest known titanotheres, *Lambdotherium* (D) and *Eotitanops* (E), the upper molars had already attained the bunoselenodont pattern, having two low, subconical internal cusps and two very large external V-shaped cusps. The probable mode of origin of this pattern is, however, furnished by certain of the Eocene condylarths (A, B, C).

A, *Protogonodon*, a basal Eocene condylarth. In this stage the molar is nearly triangular and the primitive tritubercular pattern is still evident. All the cusps are low; the protoconule and metaconule are well developed. The hypocone (hy) is just growing up from the cingulum.

B, *Euprotogonia*, another basal Eocene condylarth. In this animal the hypocone is more progressive, so that the tooth is becoming subquadrate.

C, *Ectocion*, a lower Eocene condylarth. This stage shows the assumption of the V-like form of the crest of the paracone and metacone, the reduction of protocone and metaconule, the origin of the mesostyle, and the incipiently V-shaped form of the hypocone.

D, *Lambdotherium*, a lower Eocene aberrant titanothere. The mesostyle is now well developed, and the crests of the paracone and metacone are completely V-shaped. The parastyle is strong, the metaconule is much reduced, and the hypocone is now subequal to the protocone. The paracone and metacone have also shifted inward toward the center of the crown. All the cusps have retained their low or bunoid form.

E, *Eotitanops*, a lower Eocene true titanothere. The molar pattern is now definitely titanotheroid. The protoconule and metaconule are vestigial, but the main outer cusps (*pa*, *me*) are still low.

F, *Manteoceras*, a middle Eocene titanothere. In this stage the anteroposterior diameter of the molar is considerably increased, the tips of the paracone and metacone are shifted well in toward the middle of the crown, the whole outer wall of the tooth has become considerably deeper, the protoconule and metaconule have practically disappeared, and the protocone and hypocone are low, rounded cusps.

G, *Brontotherium*, a lower Oligocene titanothere. Marked intensification of the tendencies noted under F. Paracone and metacone tips at the center of the crown, outer wall of tooth much elongated, anteroposterior diameter for the molar increased. This completes the transformation of a tritubercular molar, with simple conical cusps, into a quadrangular and bunoselenodont quadritubercular molar, with W-shaped ectoloph and low, conic internal cusps.

ters in the Condylarthra and that the perissodactyls sprang from some unknown, possibly Asiatic, larger-brained form, which in all its dental and skeletal characters would fall under the Condylarthra as here defined.

EOCENE CONDYLARTHRA NONPERISSODACTYL

Thus in the opinion of Matthew (1897) and Gregory (1910) the Perissodactyla sprang from unknown primitive Condylarthra of Cretaceous age.

The opinion of Osborn (1894–1918) is that since the known Condylarthra have specialized in a different direction from the Perissodactyla, the latter probably sprang independently from a different ungulate stock. The evidence for Osborn's opinion is in part as follows:

Euprotogonia, besides its very numerous resemblances to what we may suppose to have been the stem perissodactyl type exhibits the following differences: (1) Humerus with large entepicondyle and entepicondylar foramen; (2) carpus with lunar resting on magnum and unciform; (3) astragalus with round or convex navicular joint; (4) brain (by inference from *Phenacodus*) extremely small and smooth, with large olfactory lobes and small frontal lobes, or cerebrum.

There are thus strong differences between the most primitive perissodactyl humerus, carpus, and tarsus and those of *Euprotogonia*, *Phenacodus*, and *Meniscotherium*, which tend to support Osborn's view that the Condylarthra represent a separate specialization or radiation of their own, while the Perissodactyla sprang from an independent primitive stock, Perissodactyla primitiva, of unknown derivation but probably related to the insectivore-creodont group.

This opinion is further supported by many of the observations presented by Gregory in his "Orders of mammals," and especially by his demonstration (op. cit., p. 393) that the carpus of the ancestral Perissodactyla differs sharply from that of the known Condylarthra, a point which is fully treated below.

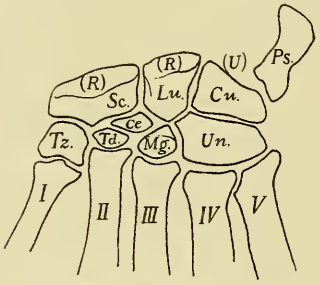


FIGURE 689.—Generalized carpus of insectivore-creodont type
After Gregory, 1910.1.

In the condylarth the head of the astragalus (navicular facet) is hemispherical and there is no facet for the cuboid; the sustentacular facet is more central in position; there is a definite constriction, or neck, between the head and the proximal end; the trochlea is wide, with low keels. In the primitive perissodactyl, on the other hand, the head, or navicular facet, is concave in the front view and convex in the side view; the sustentacular facet is vertically extended and shifted toward the middle side; there is a distinct facet for the cuboid, which meets the sustentacular facet at an open angle; the trochlea has high, sharp keels.

CONCLUSION

The remote ancestry of the perissodactyl stem, whether from "Condylarthra primitiva" or from an independent "Perissodactyla primitiva" placental stock, must be left an unsettled problem awaiting future discovery.

Skull and dental indices of certain ungulates

	Zygomatic-cephalic (bucco-cephalic)	Facio-cephalic	Premolar-molar-cephalic
Phenacodus wortmani	39?	51	26
Systemodon primaevus	47	52	30
Eohippus venticolus	41	60	30
Isectolophus	46?	56	39?
Hyrachyus	46	62	32
Triplopus	50?	53	30
Eotitanops	52	59	26
Lophiodon, ♂	41	49	30
Lambdotherium		65?	27?
Paloplotherium		62	35

NOTE.—Premolar-molar cephalic index obtained from p^2–m^3 ÷ length, premaxillary to condyle.

PRINCIPAL CHARACTERS OF THE ANCESTRAL PERISSODACTYLS

The following features characterize the ancestral perissodactyls:

1. Ungulates of small size and cursorial locomotion, alert and quick in movement.
2. Elongate limbs, narrow and stilted feet, of perfect mechanism.
3. Tetradactyl manus, tridactyl pes with reduced or vestigial fifth digit, terminal phalanges narrow and cleft distally.
4. Skull dolichocephalic, with facial region longer than cranial region.
5. Brain, visual and auditory organs, and senses well developed.
6. Eutherian dentition, $\frac{3}{3}\cdot\frac{1}{1}\cdot\frac{4}{4}\cdot\frac{3}{3}$; teeth throughout similar to those of *Euprotogonia*.
7. Diet probably succulent, tender shrubs, herbage, berries, tubers, etc.
8. Limb skeleton, humerus, carpus, and astragalonavicular joint all of perissodactyl type.

Tetradactylism in the manus of Perissodactyla is in contrast to the pentadactylism in the manus of the Condylarthra. Not a single trace of the pollex has been actually observed in any primitive Perissodactyla. That the "Perissodactyla primitiva" once possessed a pollex is attested by the presence of the extensor ossis metacarpi pollicis muscle in the tapir and horse. The homology of this muscle with that in pentadactyl mammals can not be doubted.

Tridactylism in the pes is accompanied by an occasional vestige of Mtc V (*Eohippus*).

For details of perissodactyl structures see description of skull and carpus below, and Gregory's outline (1910.1, pp. 387–395) of the principal characters of the stem Perissodactyla.

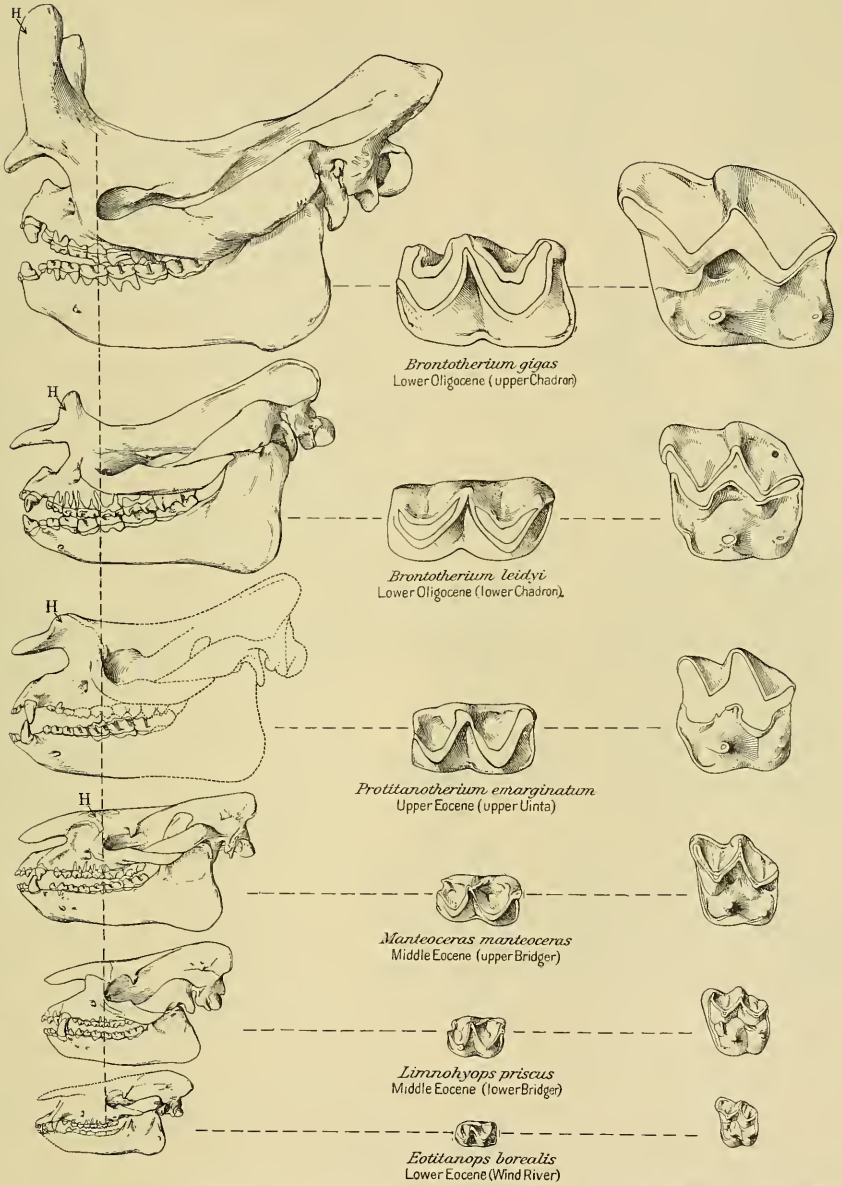


FIGURE 690.—Progressive stages of structural evolution in the skull and molar teeth of titanotheres

In *Eotitanops* the facial part of the skull is longer than the brain case (cranium). In *Brontotherium* the face is very short and the brain case very long. The horn swellings (H) first appear in *Manteoceras* and become very prominent in the succeeding stages. The top of the skull becomes deeply concave. The outer wall and the V-shaped cusps of the upper molar teeth (paracone, metacone) become very deep, and the inner cusps (protocone, hypocone) retain their low, conical form. All the lower molars retain the W-shaped crown, which increases considerably in depth.

TETRADACTYL MANUS OF PRIMITIVE PERISSODACTYLA

Tetradactylism.—The manus of the primitive perissodactyls (see fig. 692, A, B, C) differs widely from that of the primitive Amblypoda (fig. 687, B) and

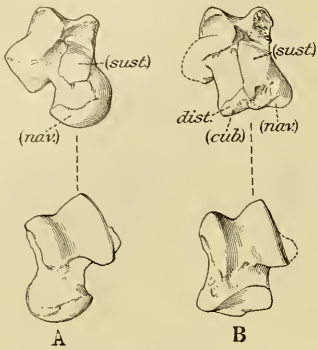


FIGURE 691.—Astragali of a condylarth, *Phenacodus primaevus* (A), and of a primitive perissodactyl, *Heptodon* (B)

primitive Condylarthra (fig. 687, C, D, E) in being tetradactyl and in the arrangement of the carpal bones. Both Amblypoda and Condylarthra—in fact, all other Ungulata, including the Artiodactyla—are pentadactyl in their most primitive forms. It had long been supposed, because of the opinions of Marsh on *Eohippus* and of Depéret (1903.1) on *Lophiodon*, that there was adequate evidence for pentadactylism in the most primitive Perissodactyla. Depéret, in 1903 (op. cit., p. 33), observed: "La patte antérieure du *Lophiodon* était certainement pentadactyle." This conclusion may perhaps rest on the presence of a small facet on the internal side of Mtc II, a facet that probably served for articulation with the trapezium, which descends secondarily on the internal side of Mtc II in the absence of Mtc I. In the most primitive manus known of *Eohippus* Granger finds a similar facet but fails to find any evidence of Mtc I either as a splint or as a vestige. Such a vestige of Mtc I may yet be discovered, but in the absence of positive evidence the primitive perissodactyl manus must be described as essentially tetradactyl.

Primitive, alternating, displaced carpals.—Osborn's error in regard to the origin of the perissodactyl foot sprang from regarding as primitive the partly displaced feet of the middle and upper Eocene perissodactyls; it now appears that these feet are mostly modified. The feet of the lower Eocene Sparnacian (=part of Wasatch) perissodactyls which have since been discovered reveal the more truly primitive perissodactyl manus, which is alternating, not serial.

This displacement is partly a cursorial adaptation. The first to comment on the real significance of the primitive displaced lower Eocene perissodactyl foot was Gregory (1910.1, p. 393), who pointed out that the manus of *Heptodon* (see fig. 692) has an extremely "displaced" carpus, the scaphocentrale completely covering the magnum, while the lunar rests entirely on the unciform. Subsequent discovery has confirmed Gregory's observation and proved that the primitive perissodactyl carpus, observed in the chalicotheres, tapirs, and titanotheres, as well as in the helaletids, to which *Heptodon* belongs, is completely displaced.

A functional classification and summary of these foot types is as follows:

Primitive tetradactyls.—The primitive condition of the perissodactyl carpus is well illustrated in Figure 700, A–E—namely, (1) magnum very small; (2) scaphoid with elongate centrale process resting on magnum; (3) lunar with a very slight magnum contact, thus resting chiefly or entirely on the unciform. This type is seen in the helaletids (A), tapirs (B), titanotheres (C), chalicotheres (E). In the most primitive horses (N) the magnum has a considerable lunar contact.

Functional isotetradactyls.—In these perissodactyls (fig. 700, D, F–J) the fifth digit is functional—that is, all four digits are used in these forms typified by *Eotitanops* (D), *Hyrachyus* (G, H), *Lophiodon* (I), and by the upper Eocene tapir *Isectolophus* (J); the magnum and lunar expand so that there is increasingly broad magnum-lunar contact; the lunar becomes wedge-shaped distally, with equal magnum-unciform facets.

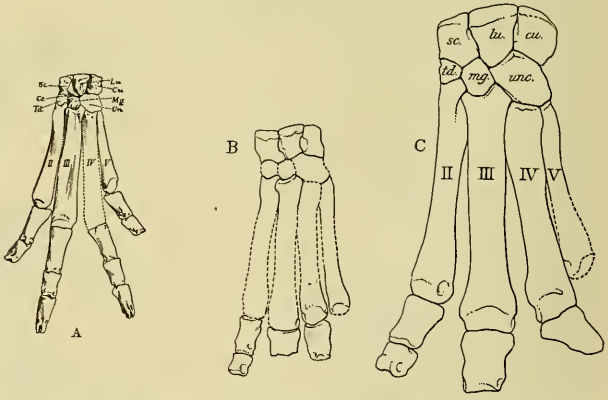


FIGURE 692.—Manus of *Heptodon*, *Lambdotherium*, and *Eotitanops*

A, *Heptodon*, Am. Mus. 294, a primitive perissodactyl manus of cursorial type. B, *Lambdotherium*, Am. Mus. 4880, and C, *Eotitanops*, Am. Mus. 296 (type), illustrate the ancestral titanothere type of manus. One-half natural size.

This type of carpus seems to be characteristic of the isotetradactyl perissodactyls. It is in wide contrast to the isotridactyl condition.

Isotridactyl perissodactyls.—In these animals (fig. 700, K, L, M) the fifth digit (D. V) is nonfunctional, reduced, or vestigial, while the remaining three digits, Mtc II–IV, equally divide the weight among them. The triplopodines, paleotheres, and helaletids develop this type of foot. It is noteworthy that in all these animals the scaphocentrale entirely covers the magnum; the lunar retains little or no magnum contact but rests mainly on the unciform; the magnum may be vertically expanded; the scaphoid is closely approximated to the unciform, so that these bones are almost or quite in contact. These isotridactyl types thus retain the primitive scaphocentrale magnum contact.

Monodactyl perissodactyls (fig. 700, N–P).—Even in the earliest Sparnacian (Wasatch) horses monodactylism is indicated by the expansion of Mtc III, accompanied by a broadening of the magnum, which, as seen in *Eohippus* (N), partly supports the lunar; as the maguum expands and flattens (O, P) the magnum-lunar contact increases. This is a condition exactly the reverse of that in the isotridactyl types, such as *Colodon* (M).

Evolution of the magnum.—This primitively small element (fig. 724, A, C, E) of the carpus is very significant in the variety of its shapes. It expands in all directions in the functional tetradactyl types, vertically in the isotridactyl types, and horizontally in the monodactyl type. Its hooklike posterior process (fig. 704) is for attachment of a tendon connected with the flexor profundus digitorum muscle (a process lacking in *Phenacodus*). The magnum is thus one of the most distinctive bones of the carpus, as stated by Gregory (1910.1, pp. 393–395). It undergoes a special and very characteristic evolution in the titanotheres. As seen from the back the lunar always rests largely on the magnum.

The manus, summary.—The discovery that in the earliest Eocene perissodactyls the scaphoid rests chiefly on the magnum while the lunar rests chiefly on the unciform proves that the Cope "taxeopod" theory of the derivation of the perissodactyl carpus from a "serial" type like *Phenacodus* must be abandoned. The primitive perissodactyl type is a displaced type; secondary types may become more or less serial. This reversal of the old and apparently well-established "taxeopod" theory has several important results. First, it tends to support the view that *Euprotogonia* and *Phenacodus* are not to be taken as ancestral types of the Perissodactyla but as independent offshoots of an insectivore-creodont stock; second, it brings out the new conception that most of the early perissodactyls were rather light-limbed, narrow-footed, cursorial animals. To this agility may have been due their wide geographic distribution, in open, semiarid country, and the acquisition of those psychic characteristics associated with speed and alertness of movement which gave them a decided advantage in competition with the small-brained Condylarthra.

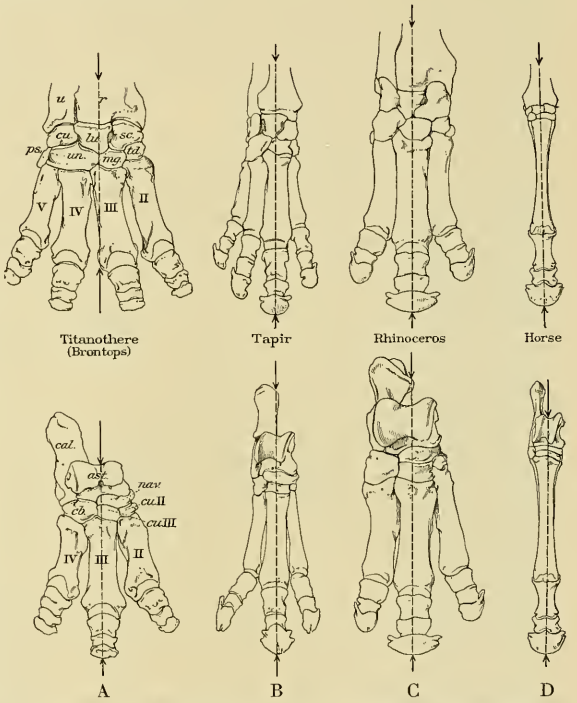


FIGURE 693.—Fore and hind feet in odd-toed ungulates (perissodactyls)

Lower row pes, upper row manus. A, *Brontops robustus*, a titanothere; B, *Tapirus terrestris*, a modern tapir; C, *Rhinoceros* (*Opsiceros*) *bicornis*, a rhinoceros; D, *Equus*, the modern horse. In primitive titanotheres the main axis of weight, or symmetry, passes through the middle (third) digit both in the fore and the hind feet. In the later titanotheres, through spreading of the foot, the main axis in the foot as a whole presents a superficial resemblance to that of the hippopotamus, among artiodactyls. In all recent perissodactyls, however, it remains in the third digit, which finally becomes extremely large, while digits II and IV diminish or dwindle away.

The mesaxonic or anisotridactyl condition of the manus—the condition in which the median toe was somewhat larger than the two lateral toes—was acquired very early. This condition is seen in the early helaletids, tapirs, titanotheres, and chalicotheres. The functional tetradactyl or isotetradactyl condition, in which D. II–V are all functional, is more or less a secondary one, as observed in *Menodus* and *Amynodon*. The isotridactyl condition, in which the three median digits, Mtc II, III, IV, divide the weight, as observed in *Triplopus*, *Palaeotherium*, *Colodon*, is also secondary.

THE SKULL OF PRIMITIVE PERISSODACTYLA

As the vast diversity in the structure of the modern perissodactyl skull, described in Chapter I, was evidently acquired during the Tertiary period, the uniformity of skull structure in lower Eocene time is remarkable; horses, tapirs, phenacodonts, titanotheres all look alike when seen from above or from the side. (See figs. 694, 695.) As in the feet, this uniformity points irresistibly to a common ancestral form, which would be a composite of skulls A, C, D, E. The palatal and occipital views of these skulls are also similar.

Historical notes.—There is little literature on the primitive perissodactyl skull, because the materials have hitherto been so scanty.

Depéret (1903.1) made a special study of the skull of *Lophiodon*, based upon *L. leptorhynchus*, from the grès de Cesseras deposits of the Lutétien stage, equivalent to our lower Bridger middle Eocene time. This skull, while retaining seven primitive characters, correctly enumerated by Depéret (op. cit., p. 28), also contains several specialized characters, namely, broadening of the zygomatic arches, abbreviation of the face, and elongation of the cranium. In these features it is a specialized form as compared with the much more ancient lower Eocene Sparnacian skulls here examined. Depéret concluded (op. cit., p. 49) that the skull of the primitive Perissodactyla had primitive features in common with those of the Hyracoidea, the Condylarthra, and especially the Amblypoda; but he traced the origin of the perissodactyl skull back of these groups to common protungulate ancestors in Cretaceous time.

Gregory (1910.1, pp. 389–391) enumerated many primitive characters of the perissodactyl skull in addition to those enumerated by Depéret, all of which are noted below, with the exception of the designation of the "muzzle" as heavy. After a close comparison with the skull of the Condylarthra, he concludes (p. 391): "The preceding skull characters may confidently be assigned to the stem perissodactyl and are all inherited from an insectivore-creodont-condylarth plan."

The primitive perissodactyl skull is certainly closer to the condylarth plan than the primitive perissodactyl foot.

General characters.—As seen from above, the skulls of certain Insectivora, of the Condylarthra, and of most primitive Perissodactyla are strikingly uniform, or analogous, namely:

(1) Narrow, elongate proportions, constricted anteriorly; (2) small craniocerebral region; (3) capacious temporal fossae; (4) limited zygomatic arches parallel to sides of skull; (5) moderately broad orbital region, orbits open posteriorly; (6) abruptly constricted preorbital region of face, similar to that of *Solenodon;* (7) occiput narrow and overhanging the condyles. Seen from the side, we observe a striking similarity of proportion and in the contour of the cranial profile, except in the specialized skull of *Heptodon* and of *Helaletes*, namely, (8) superior cranial profile simple, arched, with sagittal crest; (9) orbit placed midway between occiput and premaxillary symphysis; (10) face sloping downward toward anterior nares; (11) occiput slightly overhanging condyles; (12) temporal fossae large, with slender zygomatic arches; (13) area occupied by grinding teeth limited.

As to proportions, the ancestral skull is dolichocephalic—that is, the basilar length greatly exceeds the zygomatic width—and it is orthocephalic—that is, the palatal and basicranial regions are in parallel horizontal planes, whereas among modernized Perissodactyla many skulls are cyptocephalic—that is, the face is upturned or downturned. Also the face slightly or considerably exceeds the cranium in length, a condition technically known as proopic dolichocephaly, or dolichopy.

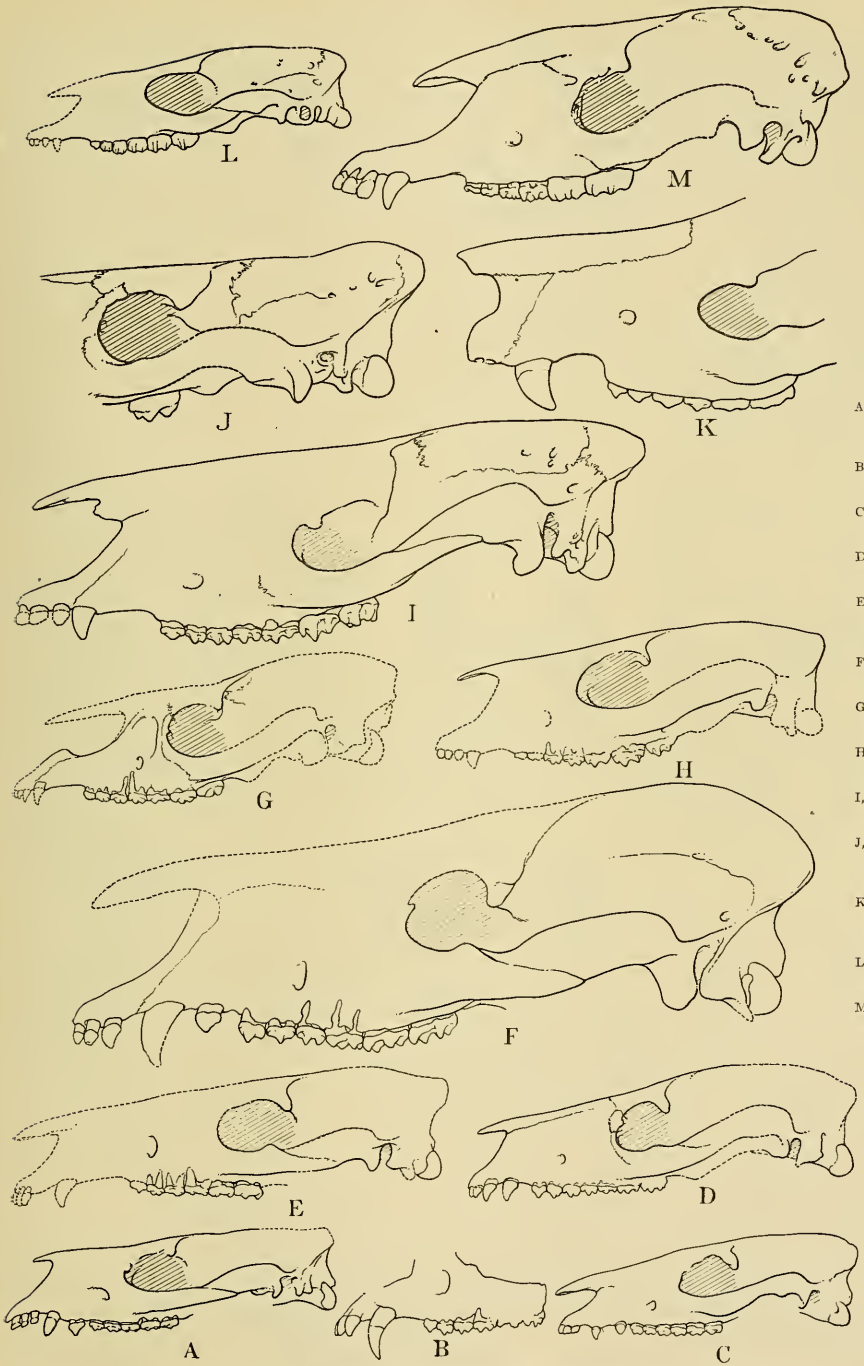
Adaptation.—The constricted anterior portion of the face, including the small terminal anterior nares and premaxillaries uniting with the nasals, indicates the presence of a long, narrow tongue, a short upper lip, limited prehension by lips, small lateral-terminal nostrils. This is in contrast to the specialized tapir-like narial region of *Heptodon* and *Helaletes* (fig. 694, B, G), in which the anterior nares are relatively more widely open or receding, with premaxillaries not reaching the nasals, distinctly lateral nostrils, and a more or less prehensile upper lip; obviously a specialized condition.

The skull suddenly expands (fig. 695, A, B, C, D, E) opposite the orbits, which are usually large and widely open, indicating alert visual powers. The senses were probably keen in these animals, although no auditory bullae or osseous tympanic tubes are observed until the beginning of the upper Eocene (*Eomoropus*, *Triplopus*).

It does not appear that the narial chamber was large, that the narial respiratory duct was very capacious, or that the olfactory chamber was large.

The sagittal crest was prominent, arched, forming the highest point of the cranium, terminating in the high, narrow occiput, which indicates that the temporalis muscle constituted the chief musculature of the jaw. The masseters, attached to the rather slender zygomatic arches, were relatively feeble. The superior borders of the zygomatic arches do not so continuously nor so distinctly connect with the lateral portions of the occipital crest, as indicated in *Lophiodon* by Depéret.

The construction of the ear region is very primitive, the external auditory meatus being widely open; the osseous portion of the tympanic, if present, was loosely attached and seldom preserved. The mastoid is



A, *Phenacodus wortmani* (Phenacodontidae), lower Eocene (Wasatch formation).
B, *Heptodon calciculus* (Helaletidae), lower Eocene (Wasatch formation).
C, *Eohippus* sp. (Equidae), lower Eocene (Wasatch formation).
D, *Systemodon* sp. (Tapiridae), lower Eocene (Wasatch formation).
E, *Lambdotherium popoagicum* (Brontotheriidae), lower Eocene (Wind River formation).
F, *Eotitanops borealis* (Brontotheriidae), lower Eocene (Wind River formation).
G, *Helaletes* sp. (Helaletidae), middle Eocene (Bridger formation).
H, *Isectolophus* sp. (Tapiridae), middle Eocene (Bridger formation).
I, *Hyrachyus* sp. (Hyrachyinae), middle Eocene (Bridger formation).
J, *Eomaropus amororum* (Chalicotheriidae), upper Eocene of Uinta Basin, Utah.
K, *Lophiodon leptorhynchus* (after Depéret) (Lophiodontidae), upper Eocene of Uinta Basin, Utah.
L, *Triplopus cubitalis* (Triplopodinae), upper Eocene of Uinta Basin, Utah.
M, *Paloplotherium* (Paloplotheriinae), upper Eocene of Uinta Basin, Utah.

FIGURE 694.—Skulls of Eocene titanotheres and other perissodactyls and one condylarth (*Phenacodus*)
Originals or reconstructions in the American Museum of Natural History. Side view. All figures two-fifths natural size.

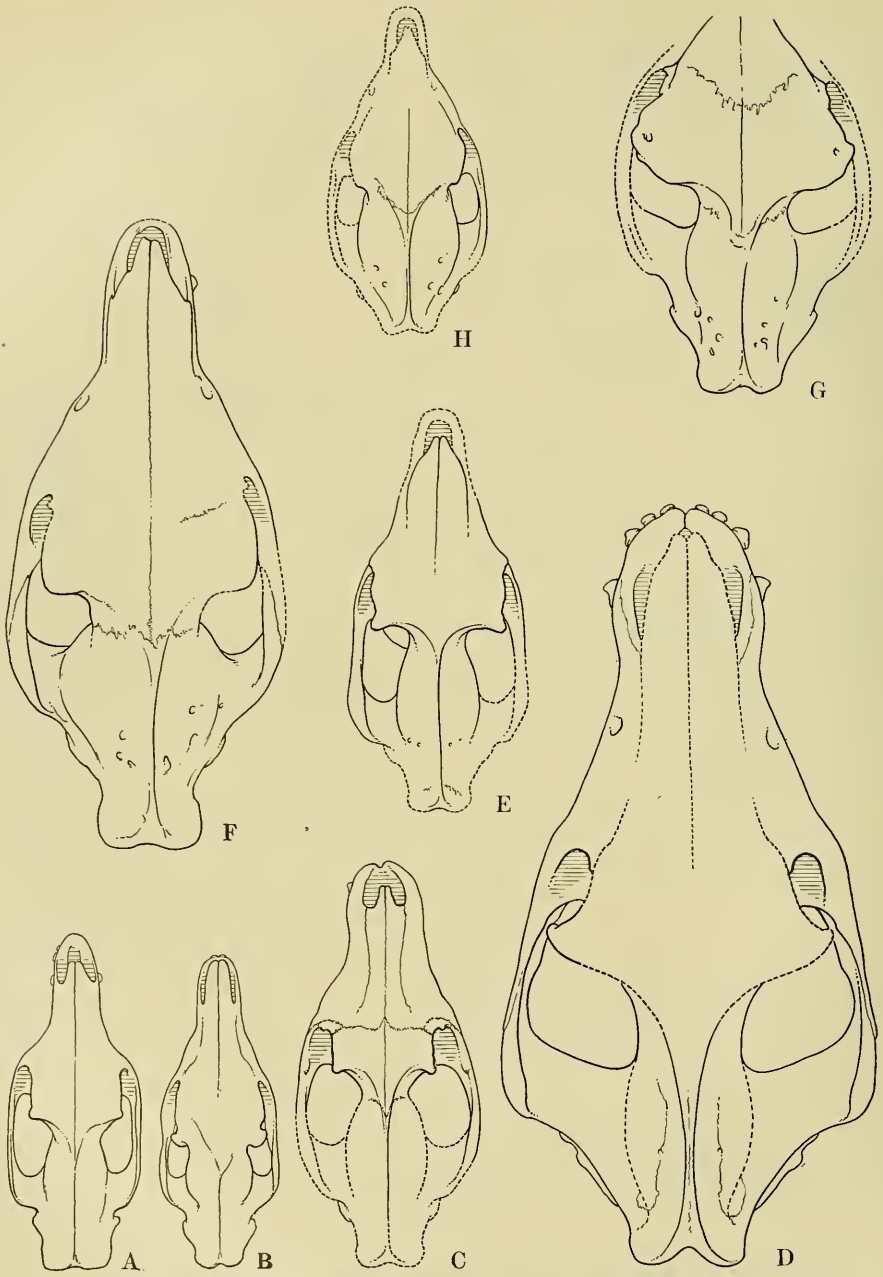


FIGURE 695.—Skulls of Eocene condylarth (*Phenacodus*) and perissodactyls

Reconstructed from materials in the American Museum of Natural History. Top views. All figures two-fifths natural size.

A, *Phenacodus* (Phenacodontidae), lower Eocene.
B, *Eohippus* (Equidae), lower Eocene (first stage).
C, *Systemodon* (Tapiridae), lower Eocene (first stage).
D, *Eotitanops* (Brontotheriidae), lower Eocene.
E, *Isectolophus* (Tapiridae), middle Eocene.
F, *Hyrachyus* (Hyrachyinae), middle Eocene.
G, *Eomoropus* (Chalicotheriidae), upper Eocene.
H, *Triplopus* (Hyracodontidae), upper Eocene.

exposed. It is only in upper Eocene perissodactyl skulls that we have found an osseous and tubular tympanic bone, as noted above.

The brain case of the cranium as seen from above (fig. 695, A, C, D) does not appear to be much larger relatively in the primitive horses and tapirs (B, C) than in the condylarths (A); the sharp constriction of the brain anteriorly seems to be as marked in *Systemodon* as in *Phenacodus*. The actual brain structure can not be known until a natural cast can be obtained.

A summary of the skull characters as observed in the various types is as follows:

Thirty primitive cranial characters possessed in common by two species of Eocene Condylarthra and by fourteen species of Perissodactyla

	Phenacodus primaevus	Phenacodus wortmani	Systemodon	Eohippus	Heptodon ventorum	Lambdotherium popoagicum	Eotitanops borealis	Eohippus venticolus	Eomoropus amarorum	Isectolophus	Helaletes	Hyrachyus	Lophiodon leptorhynchus	Triplopus cubitalis	Paloplotherium	Palaeotherium
Proportions:																
1. Dolichocephalic to mesaticephalic	×	×	×	×	×	×	×	×	×	×		×	×			
2. Cephalic-zygomatic index		39?	47	41			52			46?		46	41	50?		
3. Face longer than cranium	×	×	×	×		×	×	×		×		×				
4. Cranium longer than face													×			
5. Faciocephalic index		51	52	60		65?	59			56		62	49	53	62	
6. Orthocephalic, noncyptocephalic	×	×	×	×		×										
Facial characters:																
7. Nares small, terminal	×	×	×	×		×	×	×		×		×	×			
8. Premaxillaries joining nasals	×	×	×	×		×	×	×		×		×	×			
9. Nares receding laterally					×						×				×	×
10. Premaxillaries not joining nasals					×						×				×	×
11. Narrow antorbital region	×	×	×	×	×	×	×	×	×	×		×	×			
12. Premaxillo-maxillary symphysis compressed	×	×	×	×	×	×	×	×		×						
13. Opposite incisor series in convergent rows	×	×	×	×		×	×	×				×	×			
14. Orbits large, open	×	×	×	×		×	×	×	×	×	×					
15. Nasals slender, terminal	×	×	×	×		×	×	×	×	×		×	×			
16. Lacrimals small, exposed, with tubercles	×	×	×	×			×	×	×		×					
Cranial characters:																
17. Sagittal crest simple, arched	×	×	×	×		×	×	×	×	×	×		×			
18. Occiput narrow, high			×	×			×	×	×	×		×				
19. Zygomatic arches short, slightly expanding	×	×	×	×		×	×	×	×	×		×				
20. Postauditory region elongate	×	×	×	×		×	×	×	×	×		×	×			
21. Brain case small, contracting anteriorly	×	×	×													
22. Brain case larger, expanding anteriorly								×	×	×		×				
23. Osseous tympanic rudimentary																
24. Osseous tympanic tubular or bullate									×					×		
Palatal characters:																
25. Palate contracting anteriorly																
26. Palate straight, elongate	×	×	×	×												
27. Two anterior palatine foramina																
28. Glenoid large, shallow	×	×	×	×		×	×	×	×	×						
29. Alisphenoid canal	×	×	×	×		×	×	×	×	×		×	×			
Dental characters:																
30. Premolar-molar cephalic index		26	30	30		27?	26			39?		32	30	30	35	

From the above general descriptions and table it is clear that the prevailing or primary type of perissodactyl skull is that approached by the horse (*Eohippus*), the tapirs (*Systemodon, Isectolophus*), the titanotheres (*Lambdotherium, Eotitanops*). In this primary type we observe that the face, including the orbits, is always longer than the cranium. We may regard this as a primitive character. In the middle Eocene *Lophiodon* and all the middle Eocene titanotheres the cranium is longer than the face, a character which thus appears to be secondary.

The constricted antorbital region of the face and terminal anterior nares is also distinctive, being observed in *Phenacodus, Systemodon, Lambdotherium, Eohippus, Lophiodon, Isectolophus.* This is a primitive character. The proboscis-bearing, receding nares of the specialized lophiodonts, *Heptodon* and *Helaletes*, are secondary analogies with the tapirs, closely similar to the condition observed in *Protapirus* of the lower Oligocene.

This primitive perissodactyl skull is closely analogous or is actually related to the skull of the Condylarthra. In his detailed enumeration of the cranial characters of the primitive Perissodactyla Gregory points out (1910.1, p. 390) that this skull is of the insectivore-creodont-condylarth plan.

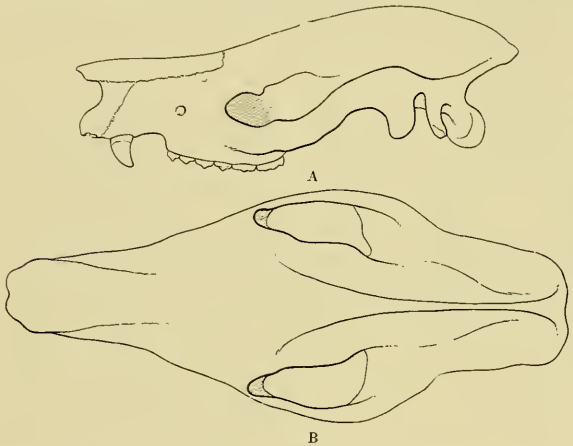


FIGURE 696.—Skulls of *Lophiodon leptorhynchus*

A, Side view; *B*, top view (of a different individual). After Depéret. One-fourth natural size.

SECTION 2. ORIGIN AND PHYLETIC RADIATIONS OF THE TITANOTHERES AND OTHER PERISSODACTYLA

The comparison of perissodactyls here made continues that begun in Chapter I with a preliminary description of the relations of the titanotheres to the chalicotheres, paleotheres, and horses in the bunoselenodont structure of their grinding teeth, as composing a great bunoselenodont branch in contrast to the great lophodont branch, which includes the tapirs, lophiodonts, and rhinoceroses, as presented in the accompanying diagrams (figs. 697, 698), showing the general and detailed phylogeny of the Perissodactyla.

SKULL OF THE PRIMITIVE TITANOTHERE

Comparison of the skull of the primitive titanotheres (*Lambdotherium, Eotitanops*) with that of the Condylarthra (*Phenacodus*) and, on the other hand, with that of all the primitive Eocene perissodactyls in which the skull is known, as shown above, reveals a striking general resemblance to the skulls of Eocene horses, paleotheres, tapirs, lophiodonts, the primitive rhinoceroses, and the chalicotheres, which is attributable to two causes, namely, similar ancestry and similar habits.

First, none of these skulls has diverged very far from the common ancestral forms; the orbit is situated midway of the head, and the face and the cranium are equal in length; the grinding teeth are short-crowned, brachyodont, and no special provision of the face is necessary for the accommodation of elongated teeth; the incisors and canines are relatively uniform in size, presenting no very striking enlargement or reduction. Second, the similarity of the skulls is due to similarity of function and adaptation. These skulls are all adapted to the browsing habit; they are the type belonging to animals of cursorial, subcursorial, and mediportal gait, the muscles of mastication occupying similar areas on the zygomatic arches and on either side of the brain case, as exhibited both in the lateral and superior views of the skulls.

In brief, the similarity in the skulls points both to similar ancestry and to analogy in habit. Nevertheless, we detect in the lower Eocene titanotheres evidences of incipient divergence, especially in the adaptation through greater or less recession of the nasal bones for the prehensile function of the upper lip. While the nasal bones are full and elongate in the titanotheres (*Eotitanops*) and in the larger of the lophiodonts (*Lophiodon*) they recede both in the smaller cursorial lophiodonts (*Helaletes*) and in the cursorial paleotheres (*Anoplotherium*). The purpose of these adaptations for the prehensile function of the upper lip, so characteristic of the modern tapirs, is to subserve the browsing function, as described in the comparison of the skull and mouth parts of the rhinoceroses in Chapter I (p. 32). This is the open-nostril type. The closed-nostril type is well illustrated in the skull of *Lophiodon leptorhynchus*, figured above, an appropriately named species, in which the nostrils are terminal and there is no room for the retractor muscles of the prehensile upper lip. In general the titanotheres conform to the latter type, with terminal nares and long nasals, but certain upper Eocene titanotheres (*Rhadinorhinus*) evolve the open nasal structure. In the two lower Eocene forms known, the cursorial *Lambdotherium* and subcursorial *Eotitanops*, the skull is of the prevailing primitive perissodactyl type, similar in proportions to that of the horse *Eohippus*, yet it forms a starting point of evolution which finally results in a type fundamentally different from that of the horse in all its proportions.

STRUCTURE OF THE FOOT IN THE TITANOTHERES AND IN OTHER PERISSODACTYLS

Fundamental characters.—The structure of the fore foot of the titanotheres is highly distinctive. It differs from that of the fore foot of all other Perissodactyla existing families of perissodactyls, the tapirs, rhinoceroses, and horses, the main weight passes directly through the center of D. III; they are mesaxonic. As shown in Figure 699 the mesaxonic extreme is the foot of the horse (*Equus*), while the paraxonic extreme is exempli-

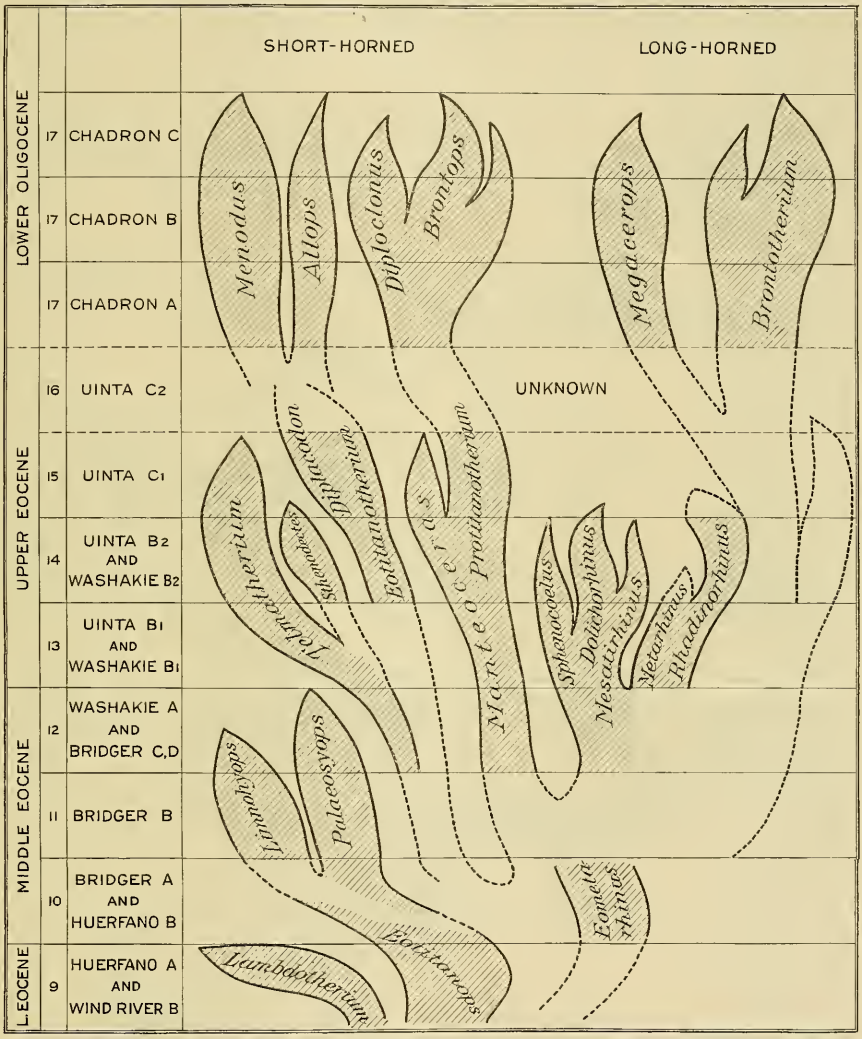


FIGURE 697.—Family tree of the titanotheres

Showing the relation between the branches (phyla), subfamilies, and genera known to science in 1919. The shaded areas show connections that are well established; the dotted lines show gaps that remain to be filled by future discovery, especially in the Uinta formation, Utah.

except *Amynodon* in its paraxonic character, owing to secondary tetradactylism and to the enlargement of the functional fifth digit (D. V). Thus the main axis of weight, indicated by arrows, passes partly between D. III and D. IV, as in the Artiodactyla, whereas in all the fied in the deer (*Cervus*). In the tridactyl pes of the titanotheres the mesaxonic condition is exactly like that of the tapirs and rhinoceroses, presenting a uniform contrast to the paraxonic condition of the pes in all the Artiodactyla (*Oreodon, Sus, Dorcatherium, Cervus*).

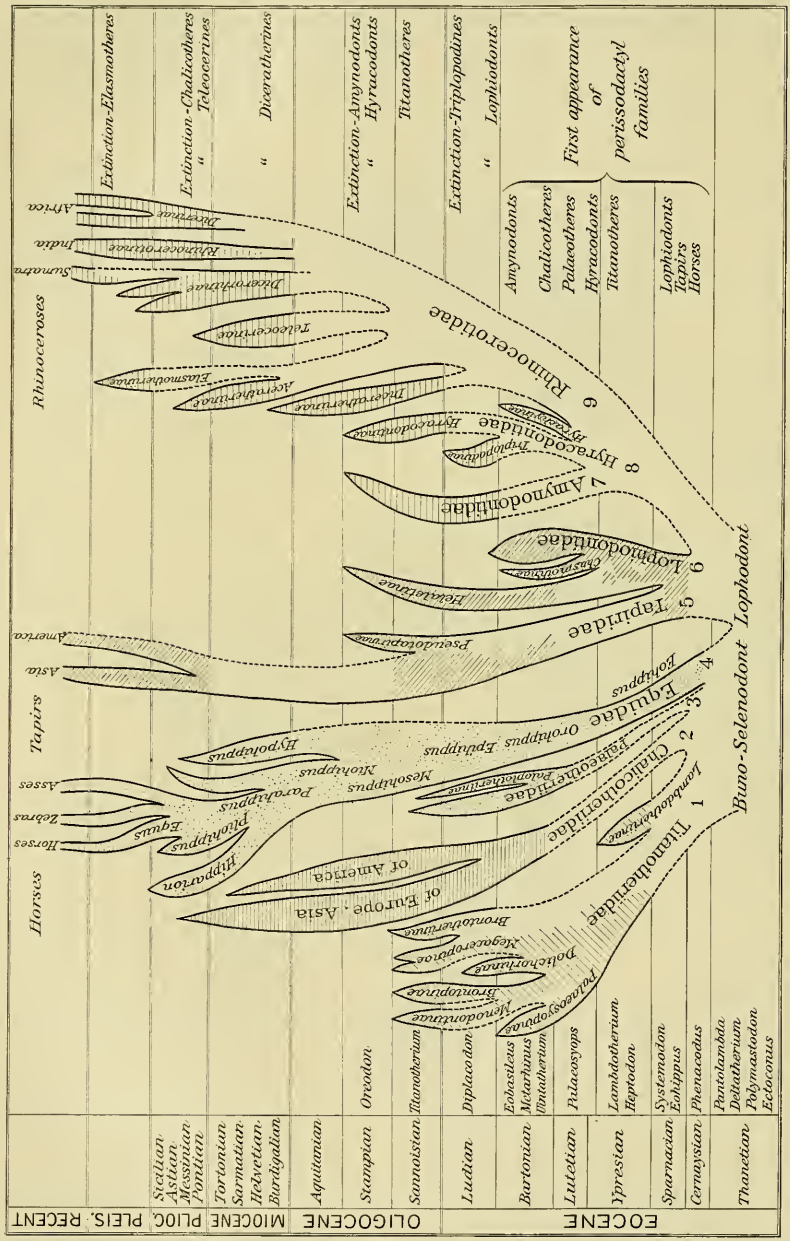


FIGURE 698.—Family tree of the Perissodactyla

Showing the successive appearance in latitude 40° of representatives of the nine families, the successive extinction of six families, and the survival of the three existing families—the horses, tapirs, and rhinoceroses

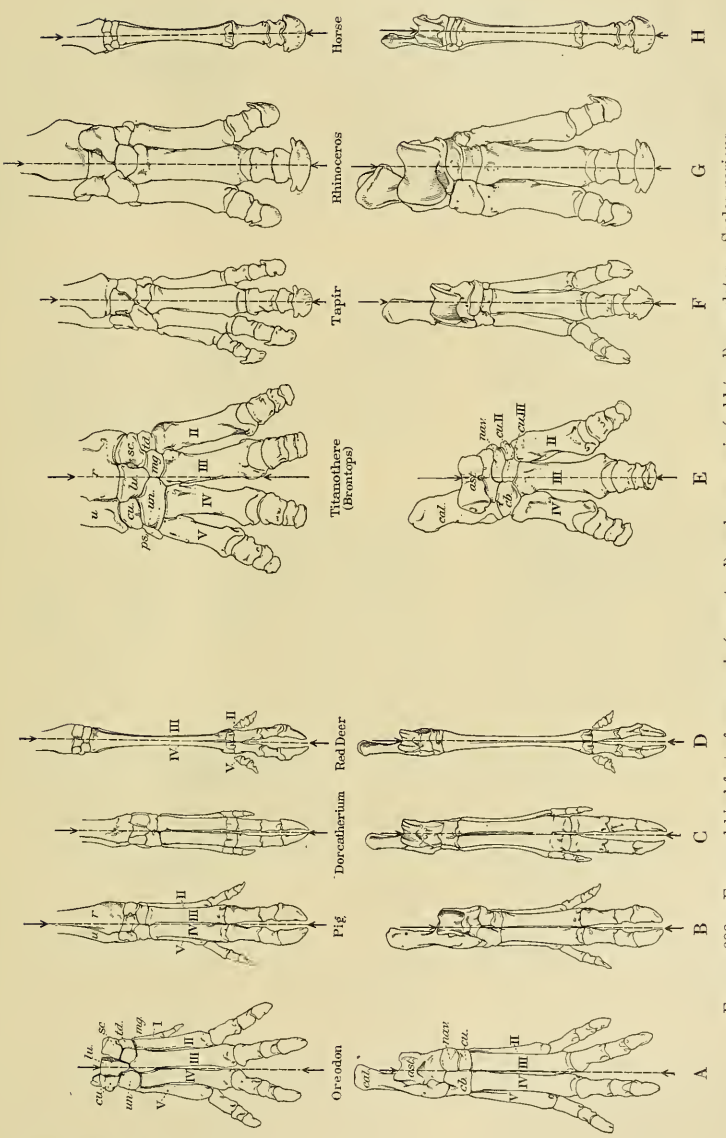


FIGURE 699.—Fore and hind feet of paraxonic (even-toed) and mesaxonic (odd-toed) ungulates. Scales various

Artiodactyls: A, *Oreodon*, a primitive artiodactyl of the Oligocene epoch; B, *Sus*, the modern pig; C, *Dorcatherium*, a primitive tragulino ruminant; D, *Cervus*, a modern deer. In artiodactyls the axis of weight, or symmetry, passes between the third and fourth digits both in the fore and hind feet. In ruminants the third and fourth digits become closely appressed and symmetrically disposed with reference to the midline. The foot becomes greatly elongated and the lateral digits (II and V) greatly reduced.

Perissodactyls: E, *Brontops robustus*, a titanothere; F, *Tapirus terrestris*, a modern tapir; G, *Opsiceros bicornis*, a rhinoceros; H, *Equus*, the modern horse. In primitive titanotheres the main axis of weight, or symmetry, passes through the middle (third) digit both in the fore and the hind feet. In the later titanotheres, through spreading of the foot, the main axis in the fore foot, as a whole, presents a superficial resemblance to that of the hippopotamus among artiodactyls. In all recent perissodactyls, however, it remains in the third digit, which finally becomes extremely large while digits II and IV diminish or dwindle away.

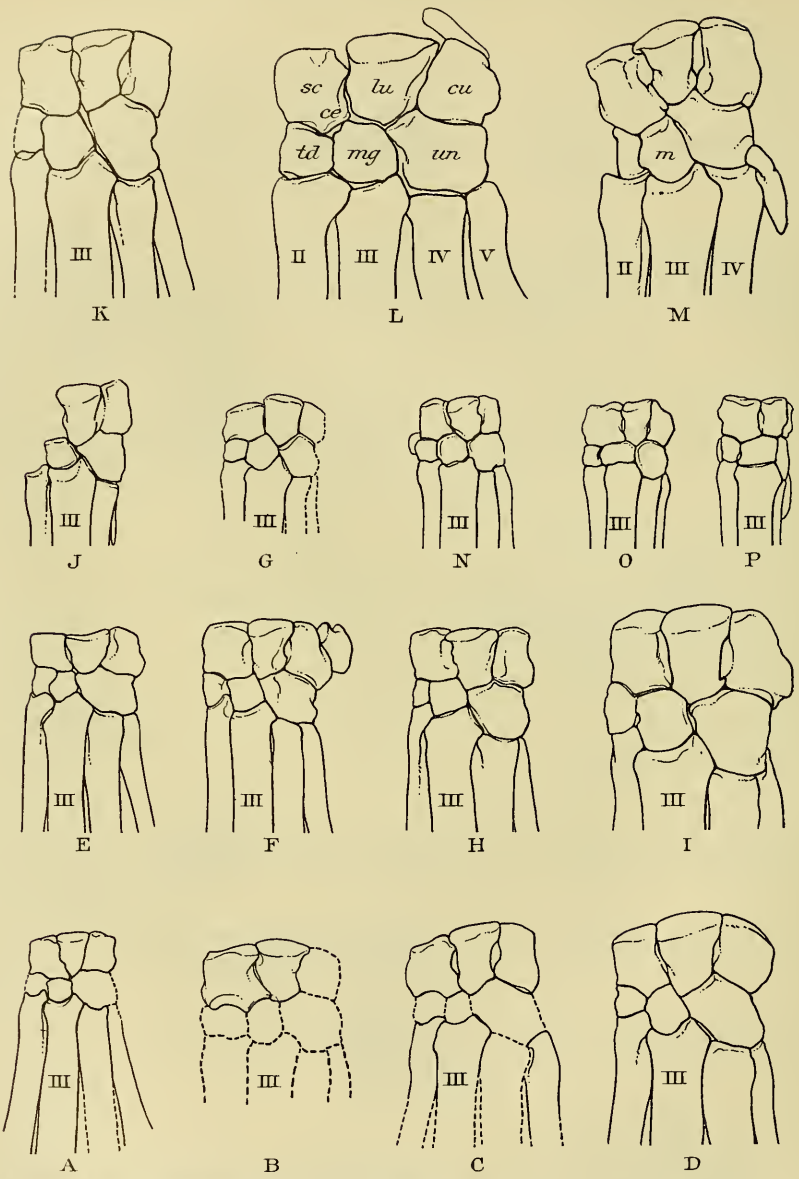


FIGURE 700.—Carpus of the Eocene perissodactyls (horses, tapirs, lophiodonts, paleotheres, and rhinoceroses)

Primitive tetradactyl; magnum small, covered by large "centrale" process of scaphoid; little or no contact with lunar in front; contact normal in back:
A, *Heptodon calciculus*, Am. Mus. 294 (Lophiodontidae), lower Eocene.
B, *Systemodon primaevum*, Am. Mus. 15807 (Tapiridae), lower Eocene.
C, *Lambdatherium papoagicum*, Am. Mus. 4880 (Brontotheriidae), lower Eocene
D, *Eotitanops princeps*, Am. Mus. 296 (Brontotheriidae), lower Eocene.
E, *Eomoropus amararum*, Am. Mus. 5096 (Chalicotheriidae), middle Eocene.
Functional tetradactyl; magnum increasing, "centrale" process of scaphoid becoming reduced, lunar-magnum contact increasing:
F, *Isectolophus* sp., Am. Mus. 12219 (Tapiridae), middle Eocene.
G, *Isectolophus annectens*, Princeton Mus. (Tapiridae), middle Eocene.
H, *Hyrachyus*, Am. Mus. 12664 (Hyracodontidae), middle Eocene.
I, *Hyrachyus*, Am. Mus. 1602 (Hyracodontidae), middle Eocene.
Isotridactyl; magnum vertical, narrow, lunar-magnum contact diminishing:
J, *Triplopus cubitalis*, Am. Mus. 5095 (Triplopodinae), middle Eocene.
K, *Colodon*, Am. Mus. 658 (Helaletidae), middle Eocene.
L, *Lophiodon*, after Depéret, Lyons Mus. (Lophiodontidae), middle Eocene.
M, *Palaeotherium*, after De Blainville (Palaeotheriidae), middle Eocene.
Monodactyl; magnum broadening, lunar-magnum contact increasing:
N, *Hyracotherium* (Equidae), lower Eocene.
O, *Epihippus* (Equidae), middle Eocene.
P, *Mesohippus* (Equidae), lower Oligocene.

The structure of the titanothere pes is typically perissodactyl, whereas the structure of the titanothere manus is comparable rather to that of the artiodactyl (even-toed) type.

The retention of D. V in the titanotheres is probably due to the early evolution of a graviportal stage, out of more primitive mediportal and subcursorial stages.

Classification by foot structure.—In devising the nomenclature of the hind foot to signify the uneven number and uneven arrangement of the digits the perissodactyl branch of the Ungulata, including the titanotheres, has been variously termed the Perissodactyla by Owen (1848.1), the Imparidigitata by Rütimeyer (1865.1) and by Burmeister (1867.1), gested by Marsh, because while in the hind foot the main weight passes through the middle toe and is therefore mesaxial, in the fore foot of many but not all of the titanotheres the main weight is distributed between the third and fourth toes and is therefore paraxial, although not so distinctly so as in the hippopotamus.

Among the amynodonts (amphibious rhinoceroses) we also observe the four-toed structure of the fore foot as in certain titanotheres. To reach the real meaning of this four-toed structure of the fore feet we compare the titanotheres with the most primitive known direct ancestors of the horses, tapirs, and rhinoceroses. We find that these also are four toed and more or less

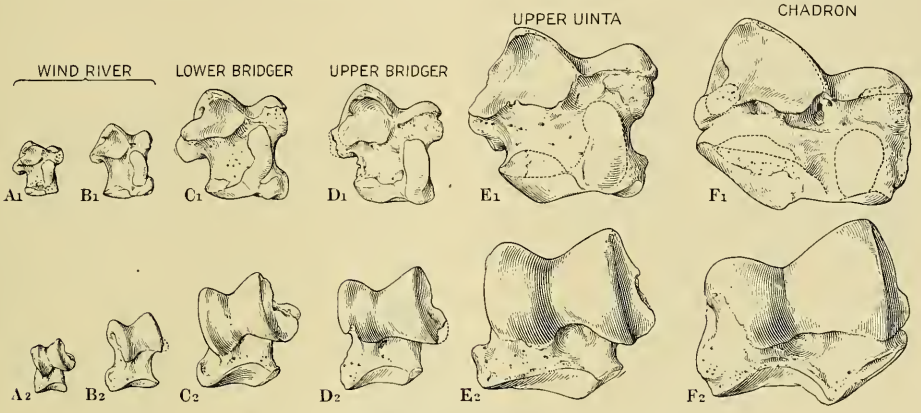


FIGURE 701.—Evolution of the astragalus in the titanotheres

Upper row, back view; lower row, front view.

A, *Lambdotherium* sp., Am. Mus. 14921, lower Eocene, Wind River formation.
B, *Eotitanops borealis*, Am. Mus. 14888, lower Eocene, Wind River formation.
C, *Limnohyops monoconus*, Am. Mus. 11689, middle Eocene, lower part of Bridger formation.
D, *Manteoceras manteoceras*, Am. Mus. 1587, middle Eocene, upper part of Bridger formation.
E, *Protitanotherium superbum*, Am. Mus. 2030, upper Eocene, Uinta C, true Uinta formation.
F, *Menodus giganteus*, Am. Mus. 505, lower Oligocene, upper *Titanotherium* zone (Chadron C).
This series shows the progressive widening of the astragalus in the transition from cursorial to graviportal habits. The earlier members have the trochlear keels high and angulate, the neck well defined, the cuboid facet very small, the sustentacular facet long and narrow. The latest members have the trochlear keels low and rounded and the head sessile, the constriction, or neck, being nearly obliterated. The cuboid at this stage is very wide, the sustentacular facet short and wide.

after the principles of classification of the French paleontologist De Blainville (1816.1), and the Mesaxonia by Marsh (1884.1).

In seeking the relations of the hoofed animals (Ungulata) Richard Owen, who followed the distinctions in foot structure first pointed out by De Blainville between the "pachydermes à doigts pairs" (number of digits even) and the "pachydermes à doigts impairs" (number of digits odd), might have found the isolated fore foot of an Oligocene titanothere a difficult subject. De Blainville's distinction between an odd or even number of digits at first appears to fail, as the fore foot of the titanotheres is four-toed, or paired, broadly resembling that of the hippopotamus. It is no less difficult to apply to the fore feet the distinctions mesaxonic and paraxonic sug- paraxonic in the fore feet, which proves that the fore feet of the titanotheres are in one sense a persistent primitive element, because they retain the fully functional outside toe of the primitive five-toed foot.

The primitive titanothere pes is very similar to that of the other primitive Eocene perissodactyls. All these animals are in a cursorial or subcursorial stage of evolution. The progressive titanothere pes shown in Figure 701 is in the graviportal stage, in which the astragalus is flattened and rests broadly on the cuboid. It thus resembles the astragalus of the graviportal rhinoceros rather than that of the mediportal tapir, in which the astragalus has a narrow footing on the cuboid, and bears no resemblance at all to that of the horse, in which the astragalus has entirely lost its anterior footing on the

cuboid. The cursorial, mediportal, and graviportal proportions and articulations of the astragalus constitute an invariable feature of the adaptive radiation of the perissodactyls into these respective types of locomotion. They are correlated with the cursorial types of limb, pelvis, and shoulder girdle structure, which have been fully described in Chapter IX in the summary of cursorial and graviportal proportions of limb segments in ungulates (p. 739).

In his studies on the evolution of the ungulate foot Osborn (1890.51) pointed out that the shape of the facets between the astragalus, calcaneum, and cuboid are distinctive in each of the perissodactyl families. The original distinctions, however, tend to be obscured by the convergent influence of the respective adoption of the cursorial, the mediportal, or the graviportal gait. The primitive arrangement of these facets in the Perissodactyla is possibly derived from the arrangement seen in the Condylarthra (*Phenacodus*), which, in turn, is an inheritance from clawed ancestors in which (*a*) the digits spread apart, (*b*) the astragalus and calcaneum diverge distally, and (*c*) there is no contact of the astragalus upon the cuboid and no astragalocuboid facet (W. K. Gregory, 1905, MS.). In the primitive Perissodactyla the progressive development of cursorial habits caused the long axes of the calcaneum and astragalus to become more parallel, so that these bones articulated distally as well as proximally.

The subsequent evolution of these astragalocalcaneal facets depends upon the following conditions: (1) Reduction of lateral digits in the monodactyl *Equus* makes for immobility between the astragalus and calcaneum; (2) the tibio-astragalar joint is more mobile than in the succeeding mediportal and graviportal forms; (3) the extent of the astragalocalcaneal facets depends partly upon the shape of the tibia and fibula above and of the supporting elements, the cuboid and navicular, below; (4) the size and direction of pull of the ligaments of the limb and foot; (5) the shape and arrangement of the astragalocalcaneal facets and adjacent parts condition the degree of rotary, vertical, and horizontal motion between the astragalus and calcaneum; (6) two general types are observed—(*a*) the astragalus with oblique distal extremity, correlated with movability, (*b*) the astragalus with truncate distal end, correlated with less movability.

In general the perissodactyl astragalus is much more movable upon the calcaneum than the artiodactyl astragalus. The horse alone has developed a comparatively rigid astragalocalcaneal union, by a system of interlocking joints and by the arrangement of the facets in three planes, more or less at right angles. This rigid astragalus is adapted to the elongate cannon bone (as in Artiodactyla), also to the reduction of the lateral digits.

MECHANICS OF THE PERISSODACTYL MANUS

Steps in evolution of the manus.—In the stem Perissodactyla we observe that (1) elevation from the plantigrade to the digitigrade position of the manus has already taken place in the ancestral stages, and there remains the transformation into the extreme unguligrade position shown in the Equidae; (2) atrophy or transposition of the muscles of rotation, of pronation, and of supination has also taken place, the muscles involved in fore-and-aft movement again reaching their highest development in the Equidae; (3) extreme reduction of the pollex has already taken place, for not a vestige of Mtc I has yet been discovered, although there is some evidence that it may have existed; (4) reduction of the trapezium follows, although this element is still retained in all primitive perissodactyls; (5) coalescence of the centrale with the scaphoid has already taken place, followed by a reduction of the centrale process of the scaphoid; (6) no "displacement" or slipping of the first and second row of carpals takes place, as Cope believed; (7) there is either growth and enlargement or reduction of several elements of the carpus, correlated with the expansion of the radius and the reduction of the ulna above and with the distribution of the weight through a diminishing number of the metacarpals below; (8) at each stage of reduction the functional tridactyl, isotridactyl, and monodactyl condition has its distinctive type of correlated carpal structure; (9) displacement of Mtc II against the magnum, of Mtc III against the unciform, the "alternating type" of displacement of Osborn, is a universal feature of the perissodactyl carpus.

The mechanics of reduction and displacement, as worked out by Ryder (1877.1), Cope (1887.1), and Osborn (1890.51), require complete restudy in view of the fact that the primitive perissodactyl carpus is of the displaced type.

The law enunciated by Osborn in 1890 (op. cit., p. 568) is, however, probably in the main correct, namely:

The direction and degree of intercarpal displacements are adapted to the gradual alteration of the major axes in the bones of the forearm and of the metapodium, respectively, as brought about by enlargement and reduction, and tend to maintain these proximal and distal axes in the same vertical line.

Carpus of cursorial, mediportal, graviportal types.—Like the bones of the tarsus, every bone of the perissodactyl carpus has its peculiar form, adapted to graviportal, mediportal, subcursorial, or cursorial locomotion. It is notable that the ancestors of each of the lower Eocene families have the cursorial type of carpus, in which the lunar rests mainly upon the unciform, with small, lateral contact on the magnum. Thus in *Eotitanops* we observe an arrangement of the carpals somewhat similar to that in the subcursorial

Hyrachyus; yet from this type has been derived the heavy graviportal manus of *Brontops*, in which the

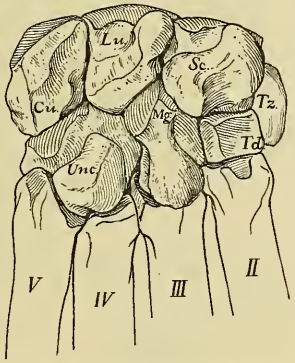


FIGURE 702.—Back view of the carpus of a middle Eocene titanothere

Mesatirhinus petersoni, Princeton Mus. 10013. Showing the lunar as the keystone of the proximal row of carpals and of the magnum and unciform, on which it rests. In front view it is largely displaced on the unciform. Each bone of the second row of carpals (for example, the magnum) forms the keystone between one of the proximal row and one or more of the metacarpals.

lunar rests broadly on the magnum. Similarly, the carpus of *Lambdotherium* is of the cursorial type, all the elements high and narrow, the lunar resting by very small contact on the small magnum. What little is known of the primitive tapir (*Systemodon*) shows a similar subcursorial structure, while the primitive lophiodont (*Heptodon*) shows a markedly cursorial carpus, in which the lunar has no contact with the magnum in front. The adaptive mechanical principles involved are explained by Osborn in his "Evolution of the ungulate foot" (1890.51). In Figures 722, 723 it is shown that as the animal passes from the cursorial into the mediportal condition (*Tapirus*, *Limnohyops*, *Palaeosyops*) the lunar broadens and gains a facet on the broadening magnum. In extreme graviportal forms (*Brontotherium*, *Rhinoceros*) the carpus is very broad, the magnum is flattened and supports half the weight of the lunar.

Adaptation in the magnum carpi.—Each carpal, like each tarsal, mirrors the primitive cursorial, mediportal, or graviportal locomotor stage of the limb. As shown below, the magnum alone mirrors the entire locomotor evolution of the titanotheres from *Eotitanops* to *Brontotherium*. The cursorial adaption at the back of the magnum is the deep hook forming the long arm of a lever in flexing the carpus, well developed in cursorial forms, also in the mediportal tapir, in *Mesatirhinus*, and in the long-footed rhinoceroses. This hook is progressively reduced as an adaption to weight in the graviportal brontotheres. In the back view of the carpus of the middle Eocene titanothere *Mesatirhinus petersoni* the magnum with its long

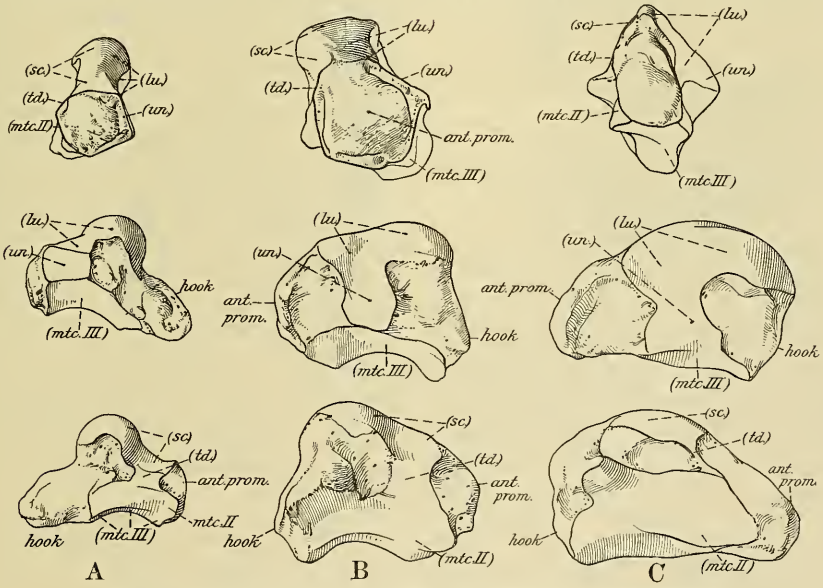


FIGURE 703.—Left magna of an Eocene titanothere and two chalicotheres

A, *Palaeosyops leidyi*, a titanothere; B, *Moropus* sp., and C, *Macrotherium* sp., chalicotheres. Top row, front view; middle row, outer side; lower row, inner side. In the chalicotheres the front face of the magnum becomes extremely high and compressed. The magnum becomes very deep anteroposteriorly, and the posterior process becomes confluent with the dorsal facet. In spite of these differences the ordinal kinship of titanotheres and chalicotheres is only partly disguised in the magnum.

hook is seen to support half the lunar, while in the front view of the same carpus the lunar rests mainly on the unciform. In further special studies of the magnum Gregory has compared the magna of *Palaeosyops* and of two chalicotheres (*Moropus* and *Macrotherium*) which display family differences and ordinal resemblances, as shown in Figure 703.

Reduction of digit V in the manus.—To the primitive cursorial habit of the perissodactyl ancestors is probably attributable the early reduction of D. I, no vestige of which has thus far been discovered in any perissodactyl, living or fossil, as pointed out above. Digit V suffers incipient reduction as the manus is raised into the unguligrade position, in which the main weight rests upon the horny sheaths of the terminal phalanges, supported by the posterior foot pad, as shown in Chapter I (p. 33). This reduction does not advance very far in the titanotheres because of the early transformation of the foot into the mediportal, weight-bearing type, in which D. V becomes useful and therefore is retained. Nevertheless, some

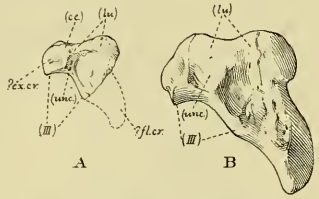


FIGURE 704.—Left magna of two lower Eocene perissodactyls

A, *Heptodon calciculus* (Cope), Am. Mus. 294; B, *Eotitanops princeps* (Osborn), Am. Mus. 296 (type). The small end faces anteriorly; the bones are seen from the outer side. Three-halves natural size. *?ex. c. r.*, Tuberosity for ?extensor carpi radialis; *?fl. c. r.*, tuberosity for ?flexor carpi radialis; (*ce.*), facet for hook of the scaphocentrale; (*lu.*), facet for lunar; (*unc.*), facet for unciform; (III), facet for Mtc III.

of the mediportal titanotheres (such as *Mesatirhinus*) exhibit a more slender D. V and a tendency toward tridactylism, a secondary mesaxonic condition of the manus, which in course of further evolution would end in a tridactyl manus. All other perissodactyls except the graviportal amynodonts (*Amynodon*, aquatic rhinoceros) rapidly reduce D. V and pass into the isotridactyl condition, with the more or less rapid reduction of D. V conditioned by the cursorial or the mediportal habit. Thus D. V persists in the mediportal *Aceratherium tetradactylum* of the Miocene of Europe, also in the modern mediportal *Tapirus*. although it disappears in the mediportal rhinoceroses, all of which become typically isotridactyl. Several cursorial branches of the perissodactyl families—the Paloplotheriinae, the Triplopodinae, the lophiodont Helaletidae, the cursorial rhinoceroses (Hyracodontinae), the subcursorial horses of the forest-living *Hypohippus* branch—all retained three digits closely compressed into a narrow, solid foot, which reaches an extreme in *Colodon*, the terminal member of the lophiodont Helaletidae.

Reduction of terminal phalanges.—Whereas in all cursorial types the terminal phalanges support relatively large horny sheaths adapted to rapid progression over hard ground, the mediportal and graviportal types tend to the enlargement of the foot pad and reduction of the terminal phalanges. Consequently in the large graviportal titanotheres, as in the Proboscidea, the terminal phalanges are greatly reduced in size, becoming almost vestigial even in such relatively swift-moving forms as *Menodus*, which has much more elongate digits and limbs than its bulky contemporary *Brontotherium*.

SUMMARY OF THE EVOLUTION OF THE PERISSODACTYL FAMILIES

The closest rivals of the titanotheres were the other perissodactyls, but the titanotheres outstripped them all until the end of lower Oligocene time. It has been noted in Chapter I (p. 24), as shown in the accompanying diagram (fig. 705), that the nine typical perissodactyl families had already diverged from one another in lower Eocene time, and that by the beginning of Oligocene time they were widely separated in their dental and osteological structure. In section 1 of the present chapter (p. 768) it has been shown that when the titanotheres, horses, tapirs, and lophiodonts first appeared in America they were so similar in structure of skull and feet that they can be separated only by careful analysis of the structure of their grinding teeth. It is not surprising that paleontologists and zoologists of the last century (Flower, Cope, Gill) were disinclined to separate them into distinct families.

The separation of the Perissodactyla according to their fundamental divergence in the structure of the molar teeth was partly suggested by Schlosser (1886.1) in his "Beiträge zur Kenntnis der Stammesgeschichte der Hufthiere und Versuch einer Systematik der Paar- und Unpaarhufer." In 1892 it was more fully developed by Osborn (1892.67, pp. 90–94) in his thesis "The classification of the Perissodactyla," in which it was shown that the main desiderata of classification are, first, clearness of phyletic relationships; second, convenience; third, structure, since it appears that in this order the teeth are more fundamental than the feet.

At this time Osborn (op. cit.) divided the Perissodactyla into 9 families and 19 subfamilies. In "The rise of the Mammalia in North America" (1893.82) Osborn extended this system, and in "The extinct rhinoceroses" (1898.143, p. 79) he showed that the Perissodactyla may be primarily divided by the fundamental pattern of the upper grinding teeth into four superfamilies, namely, Titanotheroidea, Hippoidea, Tapiroidea, Rhinocerotoidea, to which, he observed,

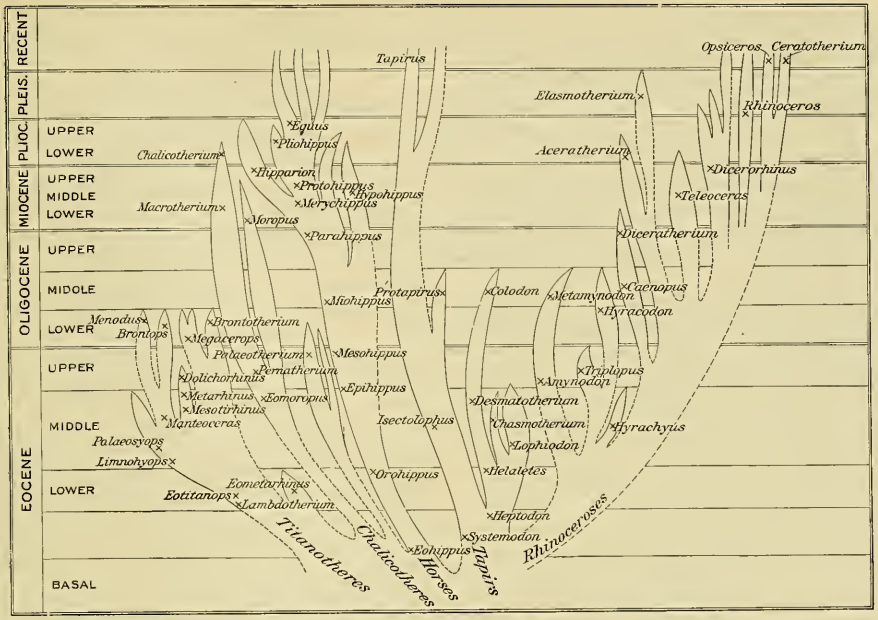


FIGURE 705.—Phylogenetic tree of the Perissodactyla, showing the superfamily, family, and subfamily branches

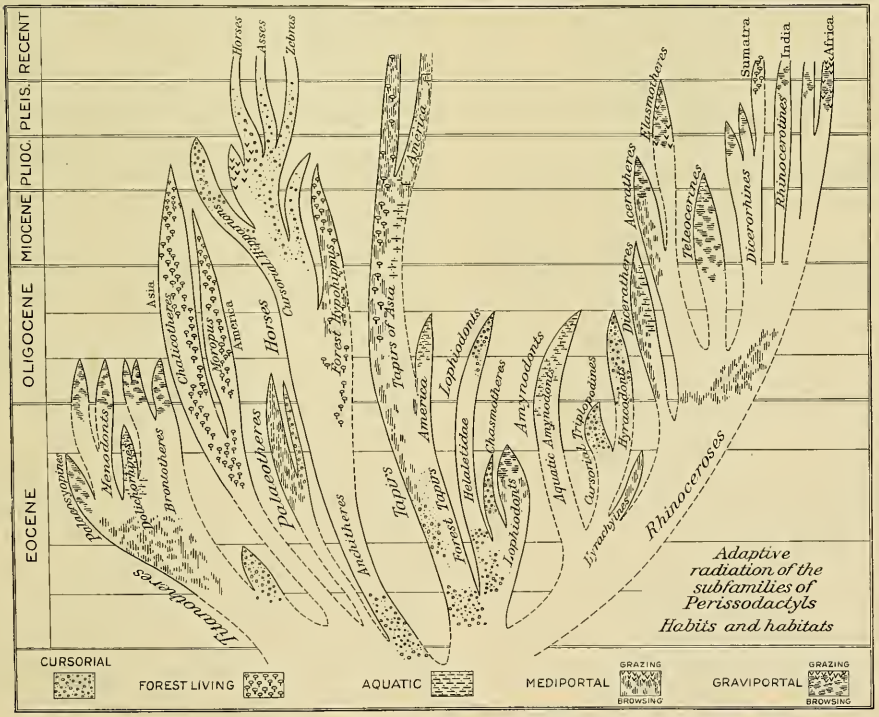


FIGURE 706.—Family tree of the Perissodactyla, showing the convergence of different branches through adaptive radiation in similar habitats and adaption to similar habits

should probably be added the Chalicotheroidea as an aberrant superfamily with molar teeth related to the titanothere pattern and perissodactyl feet provided secondarily with claws. This arrangement is substantially that which has been adopted in this monograph—that is, they have been divided into 5 superfamilies (-oidea), 9 families (-idae), 35 subfamilies (-inae). A subfamily may embrace one or more genera; it pursues an independent line of development and either terminates in an extreme or gives off a generalized branch from which another subfamily may arise.

Subsequent discovery (Osborn, 1913.398) has brought the chalicotheres more intimately within the order Perissodactyla, so that they are with some certainty now placed as a branch intermediate between the Titanotheroidea and the Hippoidea. Thus according to our present knowledge (1918) the tabular classification of the Perissodactyla is as follows:

Classification of the order Perissodactyla

A. Bunoselenodont suborder or branch:
- I. Superfamily Titanotheroidea (titanotheres):
  - 1. Family Brontotheriidae:
    - Subfamily (phylum):
      - 1. Lambdotheriinae.
      - 2. Eotitanopinae.
      - 3. Palaeosyopinae.
      - 4. Telmatheriinae.
      - 5. Manteoceratinae.
      - 6. Dolichorhininae.
      - 7. Rhadinorhininae.
      - 8. Diplacodontinae.
      - 9. Brontopinae.
      - 10. Menodontinae.
      - 11. Megaceropinae.
      - 12. Brontotheriinae.
- II. Superfamily Chalicotheroidea (chalicotheres):
  - 2. Family Chalicotheriidae:
    - Subfamily (phylum):
      - 13. Moropinae (America).
      - 14. Chalicotheriinae (Europe).
- III. Superfamily Hippoidea (paleotheres, horses):
  - 3. Family Palaeotheriidae:
    - Subfamily (phylum):
      - 15. Paloplotheriinae.
      - 16. Palaeotheriinae.
  - 4. Family Equidae:
    - Subfamily (phylum):
      - 17. Hyracotheriinae.
      - 18. Anchitheriinae.
      - 19. Protohippinae.
      - 20. Equinae.

B. Lophodont suborder or branch:
- IV. Superfamily Tapiroidea (tapirs, helaletids, lophiodonts):
  - 5. Family Tapiridae:
    - Subfamily (phylum):
      - 21. Systemodontinae.
      - 22. Tapirinae.
  - 6. Family Lophiodontidae:
    - Subfamily (phylum):
      - 23. Helaletinae.
      - 24. Lophiodontinae.

B. Lophodont suborder or branch—Continued.
- V. Superfamily Rhinocerotoidea (amynodonts, hyracodonts, rhinoceroses):
  - 7. Family Amynodontidae:
    - Subfamily (phylum):
      - 25. Amynodontinae.
  - 8. Family Hyracodontidae:
    - Subfamily (phylum):
      - 26. Hyrachyinae.
      - 27. Triplopodinae.
      - 28. Hyracodontinae.
  - 9. Family Rhinocerotidae:
    - Subfamily (phylum):
      - 29. Aceratheriinae.
      - 30. Diceratheriinae.
      - 31. Teleoceratinae.
      - 32. Dicerorhinae.
      - 33. Rhinocerotinae.
      - 34. Dicerinae.
      - 35. Elasmotheriinae.

CONVERGENCE IN HABITAT AND HABIT

It is very important to observe that although the nine typical perissodactyl families as a whole diverge and radiate from one another, the branches into which some of them subdivide under the law of adaptive radiation converge, because these seek similar habitats and assume similar habits.

Cursorial habit in the plains habitat.—Cursorial habits were independently assumed in one branch of the titanotheres, in all branches of the horses except one subfamily, in two branches of the lophiodonts, in three subfamily branches of the rhinoceroses.

Forest-living habit.—The very reverse of the cursorial plains habit was independently assumed by the chalicotheres, by the tapirs, possibly by certain branches of the titanotheres (Dolichorhininae), also by certain branches of the rhinoceroses.

Aquatic habit and river habitat.—The swamp-living and aquatic habit appears to have been assumed independently by one branch of the titanotheres (*Metarhinus*), by the amphibious rhinoceroses (Amynodontidae), and possibly by certain of the true short-footed rhinoceroses (Teleoceratinae).

Mediportal habit, browsing type.—Mediportal browsing forms are characteristic of all the middle stages of titanothere evolution, of the early stages of the lophiodonts and hyracodonts, and of all the early stages of the rhinoceroses.

Graviportal habit, browsing and grazing types.—The graviportal habit is illustrated in certain stages of the evolution of the titanotheres, in the true lophiodonts, in most of the upper Miocene, Pliocene, and Recent subfamilies of the rhinoceroses.

Secondary and independent adoption of similar habitats and habits in the different families of perissodactyls has given rise to the analogous, parallel, convergent, and homoplastic adaptations in skull, limb, and foot structure described in this chapter and in Chapter IX and has produced resemblances so close

that it may be difficult to determine the family from a single bone, and it therefore becomes necessary to determine family affinity from the teeth.

DESCENT OF THE BUNOSELENODONT FAMILIES

I, Family 1 (see table on p. 778).—When the titanotheres emerge in North America in Wind River time (lower Ypresian) they appear to have already separated into two divisions, namely, the cursorial Lambdotheriinae and the subcursorial Eotitanopinae. The subfamily Eotitanopinae is believed to have been the source of the mediportal *Limnohyops* and the graviportal *Palaeosyops* of the middle Eocene. From an unknown direct source arise the short-horned titanotheres (*Manteoceras*), which are related to the great graviportal short-horned titanotheres of the lower Oligocene (*Brontops*). Related to this stem are the forest-, swamp-, and river-dwelling Dolichorhininae. Not far from this source are the ancestors of the long-horned titanotheres (*Brontotherium, Megacerops*), which terminate in the graviportal stage and become extinct at the end of lower Oligocene time.

II, Family 2.—The chalicotheres (Ancylopoda of Cope) in skull and tooth structure appear to occupy a position intermediate between the Titanotheroidea and the Hippoidea (paleotheres and horses). At the end of middle Eocene time (upper Bridger, Bartonian) there occur the *Pernatherium* (of France) and the *Eomoropus* (of Wyoming), sharply distinguished in foot structure by the possession of powerful claws, which were probably used as weapons of defense and for grasping tree branches, since the fore limbs are not of the fossorial type. The skull and body are proportioned like the forest-living okapi, and the great rarity of remains of these animals in the plains and fluviatile deposits between middle Eocene and lower Pliocene time, comparable to the rarity of remains of forest-dwelling tapirs, points to their adoption of the forest habitat and forest-dwelling habit.

III, Family 3.—The paleotheres were probably closely related in very remote times to the horses, although they first emerge geologically in Europe in Lutetian (middle Eocene) time, their earlier history being unknown. They divide into the browsing mediportal Palaeotheriinae and the slenderly built Paloplotheriinae, which imitate the true horses.

III, Family 4.—The horses emerge as small, progressive cursorial types in Europe and America in Sparnacian (middle Wasatch) time in the genera *Hyracotherium* and *Eohippus*. There is some evidence that they subdivide in early Oligocene time into (*a*) a purely cursorial grazing type, (*b*) subcursorial browsing types, and (*c*) subcursorial forest-living types. In the types last named tridactylism is persistent in a phylum that leads into the forest-frequenting *Hypohippus*, which has crested, short-crowned teeth, functionally resembling those of the forest-living tapirs, and spreading, three-toed feet. The main line of horse evolution was into the extreme plains-living, grazing, cursorial types of hipparions, primitive and progressive horses, zebras, and asses, the latter retaining much of the browsing habit.

DESCENT OF THE LOPHODONT FAMILIES

The lophodont families spring from two great branches, the Tapiroidea (IV) and the Rhinocerotoidea (V). The families of the Tapiroidea are less uniform in the structure of their grinding teeth (Osborn, 1895.105, p. 359, fig. 6), but there is considerable evidence from the transitions in the skull, tooth, and foot structure that the Tapiridae, Helaletidae, and Lophiodontidae sprang from a common stem, the lophiodonts being closest in their grinding-tooth structure to the rhinoceroses.

IV, Family 5.—The tapirs emerge in the subcursorial *Systemodon* of the lower Eocene of America. *Systemodon* is very abundant only in the *Systemodon* zone, for throughout their entire geologic history tapiroid remains are most rare, and we assume that these animals early adopted the forest-dwelling habit and hence escaped fossilization. The American line leads through *Isectolophus* of the middle and upper Eocene, while the *Protapirus* of the lower Oligocene also represents a side branch of the main family, not typically tapiroid in its molar-tooth structure and therefore classed by Peterson with the Pseudotapirinae. The tapirs throughout their history have preserved the mediportal size and the forest, swamp, and river frequenting habitat, although high mountain dwelling forms evolve in the Andes.

IV, Family 6.—A true lophodont branch in its molar-tooth structure, known as the Helaletinae, emerges in the extremely cursorial *Heptodon* of the *Heptodon* zone of the Wasatch, as a contemporary of *Systemodon* and *Eohippus*. The skulls of *Heptodon* and *Helaletes*, we have seen, closely parallel those of the tapir in the recession of the nasal bones in adaptation to the development of a long prehensile upper lip; but the grinding teeth are exactly like those of the typical lophiodonts of the upper Eocene of Europe. The American stages are *Helaletes* of Bridger B and *Desmatotherium* of Washakie B. Unlike that of the tapirs the manus in the Oligocene stage (*Colodon*) becomes excessively elongate, slender, and highly cursorial, although persistently tridactyl. These cursorial lophiodonts were probably represented also in Europe.

The true lophiodonts (Lophiodontidae) are mediportal quadrupeds, emerging in the Sparnacian of Europe and breaking up into four independent phyletic lines (Depéret). These include the cursorial slender-limbed chasmotherines and the heavy-limbed true lophiodonts. The latter became extremely graviportal, suddenly terminating in heavy-bodied, ponderous forms in the lower Oligocene of Europe.

V, *Family 7.*—The amynodonts, a very distinct aquatic branch of the Rhinocerotoidea, are first known at the base of the upper Eocene in America and Europe, their distinctive features being very large upper and lower canine tusks (which are lost in the true rhinoceroses), broad, flat skulls, very prominent orbits, and broad, spreading, tetradactyl fore feet. The preservation of these animals in the river-channel sandstones (*Metamynodon* zone) of the lower Oligocene, their protruding orbit structure, and their spreading fore feet suggest amphibious habits. They are more aquatic than any other perissodactyls except possibly *Metarhinus* of the titanothere family.

V, *Family 8.*—The hyracodonts divide into three subfamilies, all of cursorial and subcursorial habits and of the plains and meadow habitat. The light-limbed Triplopodinae of the American upper Eocene are subcursorial. The Hyracodontinae of the lower and middle Oligocene are the most highly cursorial of all the known rhinoceroses; they are, in fact, small-headed, tridactyl, swift-running rhinoceroses. The Hyrachyinae are more conservative mediportal forms, resembling the tapir in proportions, characteristic of the middle and upper Eocene of America. They stand very close to the origin of the true rhinoceroses, if not directly ancestral to them. Apparently none of the hyracodonts found their way into Europe, though certain fossil remains of middle Europe have been referred to *Hyracodon*.

V, *Family 9.*—The true rhinoceroses suddenly emerge in two subfamilies of the lower Oligocene, namely, the pair-horned diceratheres (*Diceratherium*), of the Sannoisian and White River, of Europe and America respectively, and the hornless Aceratheriinae, animals having the same geographic range, which are distinguished by the retarded development of the median horn. These mediportal animals expand in number and variety immediately after the extinction of the titanotheres in lower Oligocene time and become the dominant quadrupeds of middle and upper Oligocene time both in Europe and America. The diceratheres became extinct in middle Oligocene time, but the aceratheres developed a middle horn on the top of the skull (Osborn, 1899.166), and it is possible that the *Aceratherium incisivum* of the lower Pliocene may have given rise to the gigantic single-horned *Elasmotherium* of the Pleistocene; but this descent is highly conjectural. In lower Miocene time the short-footed, graviportal Teleoceratinae emerge in Europe and Asia and migrate to America. In body and limb structure they even present analogies to the hippopotami but exhibit no aquatic adaptations in the skull.

The Dicerorhinae also appear in the lower Miocene of Europe and become the dominant European rhinoceroses in Pliocene and Pleistocene time, a branch surviving to-day in the existing Sumatran rhinoceros, a forest-frequenting, browsing animal, relatively primitive in cranial and dental structure, mediportal in proportions.

In the lower Pliocene of Europe also appear the Dicerinae, related to the existing African white rhinoceros *Ceratotherium simum*, which is distinctly a grazing, hypsodont, extremely graviportal type.

In the meantime the true Rhinocerotinae appear in Asia in the lower Miocene.

In the Pleistocene of Eurasia occur the steppe-frequenting, grazing, hypsodont Elasmotheriinae, gigantic animals of graviportal type, which may represent a branch from the original Aceratheriinae stock (Osborn, 1900.192).

SURVIVAL AND EXTINCTION OF THE PERISSODACTYLA

The theoretic causes of the extinction of so many branches of the Perissodactyla in early Oligocene time and the survival to the present time of only five of these branches—the Equinae, Tapiridae, Dicerorhinae (Sumatran), Dicerinae (African), and Rhinocerotinae (Indian) are discussed in Chapter XI, section 2.

PHYLETIC BRANCHING OF THE TITANOTHERES

As compared with other perissodactyls the adaptive radiation and phyletic evolution of the titanotheres is seen to be limited by their conservative grinding tooth structure and their closely correlated foot structure. The grinding tooth of the titanotheres is mechanically incapable of transformation into the grazing type; the feet do not evolve in a cursorial direction after the first essaying of cursorial structure in *Lambdotherium*. Consequently the evolution and specialization of the titanotheres took place principally within the browsing habitats of meadows, the borders of forests, and the borders of streams and rivers, the last affording amphibious and possibly aquatic habitats. In respect both to hypsodonty of the teeth, which is invariably a grazing adaptation, and to elongation of the feet for the seasonal migrations connected with grazing habits, the titanotheres are greatly inferior in plasticity to the rhinoceroses, which independently develop an extreme cursorial type (*Hyracodon*), an extreme aqnatic type (*Amynodon*), also two extreme grazing types (*Elasmotherium* and *Ceratotherium simum*).

The phyletic branching of the titanotheres is summarized in Figure 697.

SECTION 3. SUMMARY OF THE CRANIAL AND SKELETAL EVOLUTION OF THE TITANOTHERES

GENERAL CONCLUSIONS REACHED

Epitome of the evolution.—An epitome of the entire evolution of the skull, teeth, and skeleton of the titanotheres brings out three principal conclusions:

First, the evolution of the feet and limbs, as already described in detail, from the mediportal to the graviportal condition, closely parallels similar stages of

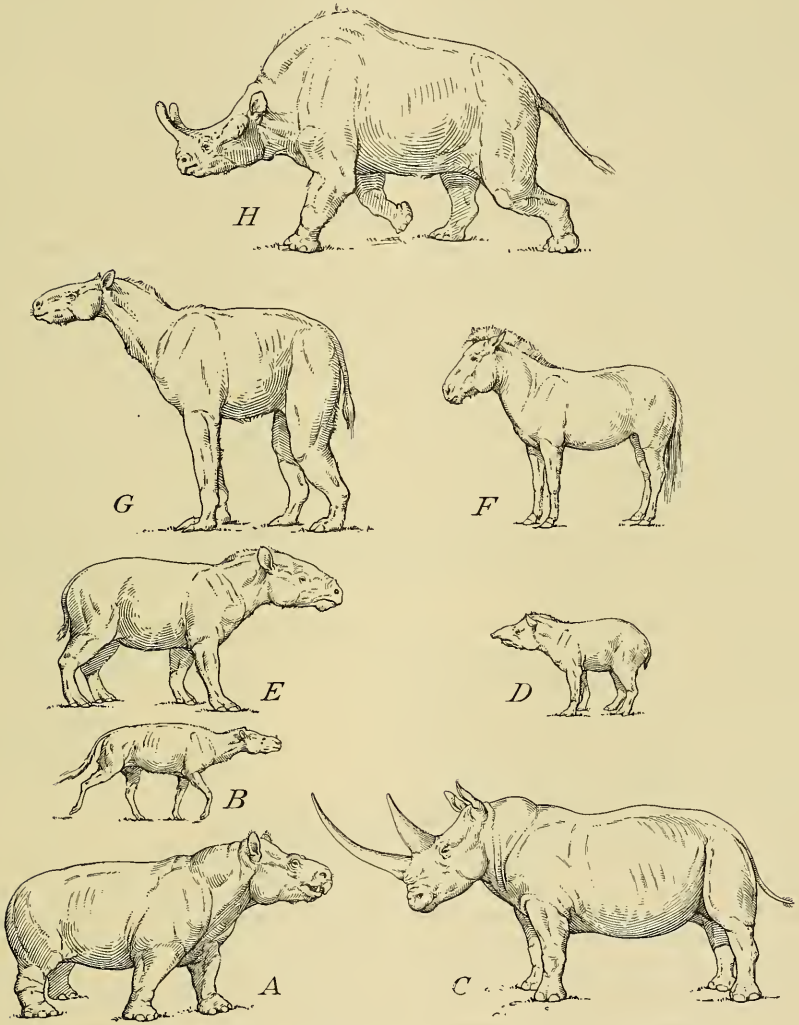


FIGURE 707.—Outlines of the body form of the perissodactyls drawn to the same scale

The largest known member of each family is selected for comparison. The animals are grouped according to their natural relationships, indicated especially by the pattern of the molar teeth, as follows:

Rhinocerotoid group: *A, Metamynodon*, family Amynodontidae, graviportal aquatic rhinoceros, lower Oligocene; *B, Hyracodon*, family Hyracodontidae, cursorial rhinoceros, lower Oligocene; *C, Ceratotherium simum*, family Rhinocerotidae, living white rhinoceros, graviportal. Tapiroid group: *D, Tapirus terrestris*, family Tapiridae, living tapir.

Hippoid group: *E, Palaeotherium*, family Palaeotheriidae, mediportal, lower Eocene; *F, Equus przewalskii*, family Equidae, living horse, cursorial.

Chalicotheroid group: *G, Moropus*, family Chalicotheriidae, clawed perissodactyl, lower Miocene.

Titanotheroid group: *H, Brontotherium platyceras*, family Brontotheriidae, graviportal, lower Oligocene.

evolution in all the other perissodactyls. This is clearly brought out in Chapter IX, sections 1–2.

Second, the evolution of the grinding teeth is decidedly inferior to that of all the other families of perissodactyls. The titanothere molar, though capable of indefinite enlargement, is not capable of transformation into a hypsodont tooth.

Third, the transformation of the skull, on the contrary, is a far more extreme specialization in the titanotheres than in the tapirs or even in the horses; it is, on the whole, more extreme than in the rhinoceroses. Consequently, cranial evolution and transformation are among the most distinctive characteristics of the titanothere family. In many characters, as pointed out in Chapter I (pp. 28–32), the cranial transformation in the titanotheres is analogous to that of the rhinoceroses; in other characters it is unique.

In brief, although the feet and teeth of the titanotheres are conservative, retaining more or less their ancestral form, the skull is extremely progressive, presenting greater variety of form and proportion than that of any other perissodactyl. In every subfamily the skull is so plastic as to be in a continuous state of transformation, radiating into great extremes of structure, which show the widest possible differences of proportion and in which all resemblance to the ancestral type is completely lost. The horns finally become the dominant feature of the skull and appear to condition the evolution of all the other parts.

The transformation of the *Eotitanops* type of skull into the *Brontotherium* type, which is epitomized in Figure 709, as compared with the transformation in other perissodactyls, shows the following principal features: (1) Loss or reduction of parts is relatively infrequent; (2) few rectigradations (new parts) arise, the only absolutely new features being the horns and additional cusps on the premolar teeth; (3) increase in bulk is enormous and with one exception is continuous and progressive in every branch; (4) changes of proportion are great in all parts of the skeleton, especially in the skull.

Loss or reduction of parts.—The known losses and numerical reductions of parts may be summarized as follows: (1) Incisor teeth ($\frac{2}{2}$) retained in some phyla (*Brontotherium, Brontops*) in more or less functional condition; incisors entirely lost ($\frac{0}{0}$) in other phyla (*Menodus, Megacerops*); (2) intermediate conules on the superior grinding teeth lost in all phyla, a loss that was the final cause of the mechanical imperfection of the teeth and of the extinction of the family, in contrast with the horses, in which the conules save the race; (3) trapezium, inner bone of the second row of the carpus, variable or absent.

Rectigradations.—New cusps and cuspules appear on the upper and lower premolar teeth, being independently developed in each of the titanothere phyla at more or less rapid rates of evolution, and osseous horns appear at the junction of the nasal and frontal bones, being independently developed in five distinct phyla and more or less rapidly evolving.

Harmonic increase in size.—During the period of time represented by the Wind River, Bridger, Washakie, true Uinta (C), and Chadron formations there was a great increase in bulk or mass of body in the titanotheres. In the smallest known true titanothere, *Eotitanops gregoryi*, the skull was smaller than that of a wolf, and the body therefore probably weighed less than 150 pounds. On the other hand, the largest titanothere certainly weighed much more than an adult black rhinoceros, whose body weight is estimated in Brehm's Tierleben as 1,600 kilograms, or 3,500 pounds. It would weigh less, however, than a large African elephant, whose estimated weight is 4,000 kilograms, or 8,800 pounds. Therefore, if we assign a weight of 2,800 kilograms, or about 6,000 pounds, to the largest titanothere its weight would have been about 40 times as great as that of its diminutive ancestor *Eotitanops gregoryi*.

Changes in proportions (*allometrons*).—Each phylum of the titanotheres has its distinctive rate of increase of the grinding area of the teeth in relation to the length of the skull, as shown in the accompanying table. Of the Oligocene phyla, *Menodus* has the relatively largest grinding area; *Megacerops* and *Brontotherium* have the relatively smallest.

Measurements, in millimeters, showing progressive increase in length of true molar series as compared with total length of skull

	Basilar length of skull	M^1–m^3	Ratio of m^1–m^3 to basilar length (per cent)
Eotitanops borealis	313	54	17
Limnohyops laticeps	[a]410	90	21
Palaeosyops major, Am. Mus. 12182	389	94	21
Palaeosyops leidyi, Am. Mus. 1544	415	100	24
Palaeosyops leidyi, Am. Mus. 1516	414	102	24
Manteoceras manteoceras, Am. Mus. 1569	492	103	20
Manteoceras manteoceras, Am. Mus. 1545, now in Nat. Mus	523	118	22
Manteoceras washakiensis, Am. Mus. 13165	[a]490	116	23
Telmatherium ultimum, Am. Mus. 2060	510	129	25
Brontotherium leidyi, Carnegie Mus. 93	665	190	28
Brontotherium gigas	830	241	29
Menodus giganteus, Field Mus. 5927	825	270	32
Menodus giganteus, Am. Mus. 505	777	250	32

[a] Estimated.

Comparison of the percentage increase of the body as a whole and of the grinding teeth as a whole shows that the increase of the grinding teeth in bulk approximately kept pace with the increase in

the bulk of the animal as a whole. Such an increase might have been expected, for it can not be said that the grinding teeth of *Brontotherium gigas* are greatly superior mechanically to those of *Eotitanops borealis*. If these grinders of *Brontotherium gigas* had been perfected through hypsodonty and plication of the enamel, as in the hypsodont horses, rhinoceroses (*Elasmotherium*), and elephants, it is obvious that the bulk of the grinding teeth need not have been so great. In other words, *Brontotherium* provided for the greatly increased size of its body by increasing the size of its grinding teeth rather than by mechanically improving them.

The above series of comparative measurements shows that in the Oligocene titanotheres the true molars (m_1^1 to m_3^3) were, relatively to the skull, of the disharmonic evolution which is in progress in all parts of the skull and teeth. The above comparisons include changes which distinguish the two generic extremes in the evolution of the family, namely, *Eotitanops* and *Brontotherium;* but the following table shows that similar changes distinguish each of the three principal phyla of the lower Oligocene, namely, *Brontops, Menodus,* and *Brontotherium.*

Each genus has its distinctive velocity in the evolution of each cranial and dental character. The researches made for this monograph have shown that the most significant diagnostic feature of a genus is the relative rate of evolution of the separate parts of which the skull and teeth are composed. For example, we observe that in *Brontops* the increases in different parts of the skull and teeth are more nearly

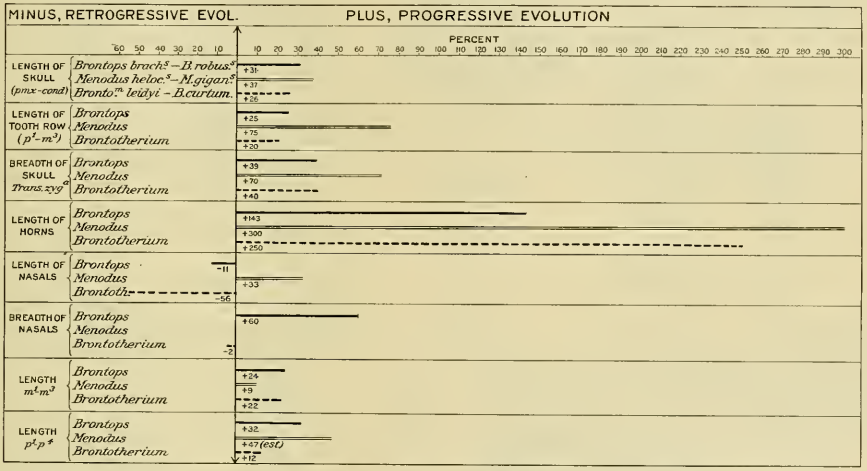


FIGURE 708.—Disharmonic evolution, progressive and retrogressive, shown in eight characters of the skull and teeth of *Brontops, Menodus,* and *Brontotherium*

Range of species from the lower *Titanotherium* zone (Chadron A) through the upper *Titanotherium* zone (Chadron C).

twice as long as in the Eocene *Eotitanops.* For example, in *Brontotherium gigas* the true molars are 29 per cent of the skull length, in *Eotitanops borealis* only 17 per cent; yet in *Menodus* the molars were even proportionately larger, namely, 32 per cent of the skull length. In the grinders as a whole the relative gain in the true molar series is, however, offset by the loss in the premolar series, for the ratio of the premolars to molars drops from 63 per cent in *Eotitanops* to 42 per cent in *Brontotherium curtum.* Yet the gain in the molar series more than offsets the relative loss in the premolar series.

DISHARMONIC EVOLUTION IN LENGTH AND BREADTH OF SKULL

The above disharmonic evolution of the true molars as compared with the skull and of the premolars as compared with the true molars is a very simple example harmonic, whereas in the related short-horned *Menodus* they are most widely disharmonic. This contrast may be summarized as follows:

Percentages of disharmonic evolution in eight characters in Brontops, Menodus, and Brontotherium

	Brontops brachycephalus	Menodus giganteus	Brontotherium curtum
Length of skull	+31	+37	26
Length of tooth row	+25	+75	+20
Breadth of skull	+39	+7	+40
Length of horns	+143	+300	+250
Length of nasals	−11	+33	−56
Breadth of nasals	+60	--------	2. 9
Length of true molars (m^1–m^3)	+24	+9	+22
Length of premolars (p^1–p^4)	+32	+47	+12

These percentages of increase and decrease are quite distinct from relative size. For example, the grinding series of *Menodus* is relatively much longer than that of *Brontotherium*, yet the percentage of increase is less during lower Oligocene time; the horns of *Menodus* are much shorter than those of *Brontotherium*, yet the percentage of increase in *Menodus* is greater.

In *Menodus* the skull gains 37 per cent in length and 7 per cent in breadth; it lengthens 30 per cent faster than it broadens.

EVOLUTION OF THE SKULL IN CORRELATION (COADAPTATION) WITH THAT OF THE TEETH AND HORNS

The skull evolution of the titanotheres passes through two great phases. The first, in the lower and middle Eocene, is in coadaptation to the grinding teeth; the second, in the upper Eocene and lower Oligocene, is in coadaptation to the grinding teeth and to the support of the increasingly powerful horns. Both these phases are affected in all their characters by progressive brachycephaly or dolichocephaly, proceeding from an original mesaticephalic condition.

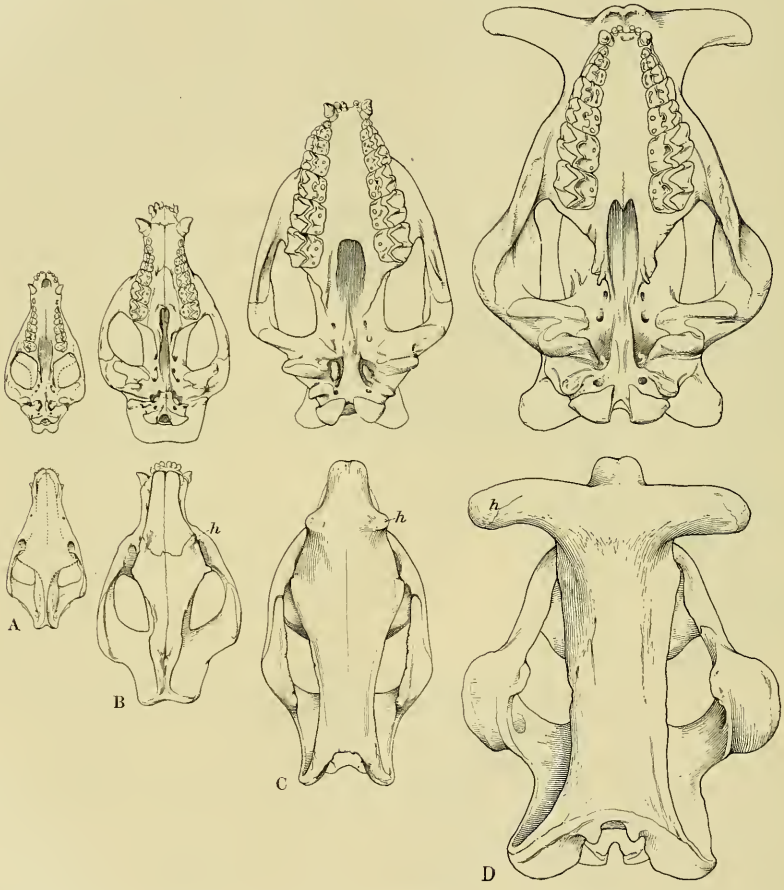


FIGURE 709.—Evolution of the skull in the titanotheres

Top and palatal views. One-twelfth natural size. A, *Eotitanops princeps;* B, *Manteoceras manteoceras;* C, *Brontotherium leidyi;* D, *Brontotherium curtum*. Note the lengthening of the cranial portion of the skull, the origin of the horn swellings and their forward displacement in front of the orbits, the widening of the occipital crests, and the spreading of the bucal process of the zygomatic arches. The palatal view reveals the progressive widening of the molar teeth, the partial molarization of the premolars, and the relatively conservative (nonprogressive) character of the base of the cranium.

The most interesting contrast is in the skulls, namely, between those which are progressively brachycephalic, like *Brontops*, and those which are progressively dolichocephalic, like *Menodus*. In *Brontops* the skull gains 31 per cent in length and 39 per cent in breadth; it broadens 8 per cent faster than it lengthens.

Eocene browsing skull phase.—In the Eocene phase we compare the primitive titanothere skull, as seen above in the synoptic plate, with the skulls of other Eocene and recent browsing perissodactyls, having short-crowned, brachyodont grinding teeth, in which there is no special modification of the nares for a prehensile upper lip. The general resemblance in proportions is quite close; the face and cranium are of equal length, the orbit is placed above the last superior grinder.

The changes that took place are profoundly disharmonic. They show progressive brachycephaly, mesaticephaly, and dolichocephaly, affecting more or less similarly all other transformations, and are as follows:

1. The cranium is greatly elongated—opisthopic dolichocephaly, dolichocrany.

2. The face is relatively abbreviated—proopic brachycephaly, brachyopy.

3. The orbits are shifted forward (displaced) from above m^3 to above p^4.

4. The horns, which originate directly above the orbits, are shifted forward to a point above the canines, in the long-horned forms especially.

5. As the horns shift forward in the long-horned forms the nasals are absorbed and relatively abbreviated.

6. The cranium is flattened and elongated both in the long-horned and short-horned dolichocephalic and mesaticephalic genera.

7. The occiput is broadened as the cranium is flattened.

8. To fill the spaces of the enlarging skull the frontal ethmoid and olfactory sinuses are greatly expanded.

9. The zygomatic arches are broadly expanded—buccal brachycephaly.

10. The auditory meatus is closed inferiorly by the approximation of the postglenoid and post-tympanic processes.

11. The dental series, expanding in upper Eocene time, is relatively constant throughout the lower Oligocene, taking up about half the length of the skull.

The above eleven changes, which are begun in the upper Eocene phyla of titanotheres, culminate in all the Oligocene phyla. In the Oligocene they represent the second phase of titanothere skull evolution, in which there is a double coadaptation to the functions of the great grinding teeth and of the horns, respectively. In coadaptation to the greater or less dominance of the grinding teeth or of the horns we find a large number of correlated and compensatory characters. For example, in *Menodus*, in which the grinding teeth are superbly developed and which show some tendency even to hypsodonty, the horns remain of moderate length, the canine tusks in compensation become enlarged and relatively effective weapons, the nasals are moderately abbreviated, and the skull as a whole is mesaticephalic, the zygomatic arches being moderately expanded.

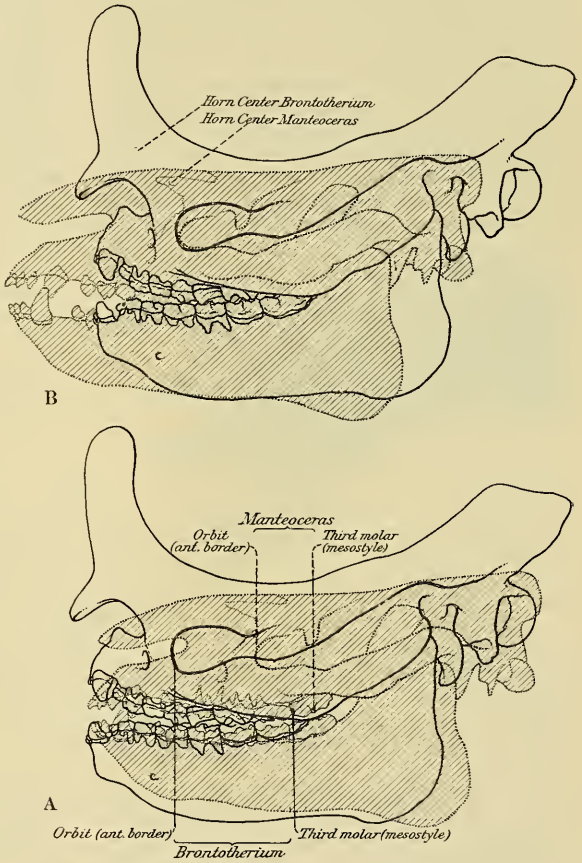


FIGURE 710.—Relative proportions of the skulls of *Manteoceras* and *Brontotherium*

Contrast in the proportions of the facial and cranial parts of the skull in Eocene and Oligocene titanotheres. Middle stage (*Manteoceras*) in dots, lower Oligocene stage (*Brontotherium*) in heavy black line. Both figures are reduced to the same absolute length from premaxillaries to occipital condyles. In A the premaxillaries and the condyles, respectively, of the two skulls are superposed, showing the forward shifting of the horns and orbits and the lengthening of the cranial region in the Oligocene type. In B the anterior rim of the orbits of the two skulls is made to coincide, emphasizing the shortening of the face in the Oligocene type.

Brontotherium presents an extreme contrast. The horns, which are greatly elongated, are the dominant character of the skull; the nasals are absorbed and abbreviated; the canine teeth are blunt and less effective as weapons; the grinding teeth evolve slowly and do not become subhypsodont; the buccal brachycephaly is very extreme.

ARE THE PROPORTIONS OF SKULL AND TEETH ADAPTIVE?

Brachycephaly, mesaticephaly, dolichocephaly.—Besides the dominance of the development of the grinding teeth and horns there is repeatedly manifested in the Eocene and Oligocene titanothere crania progressive brachycephaly, persistent mesaticephaly, and progressive dolichocephaly. The adaptive nature of these profound changes of proportion, which affect the skull as a whole, is less obvious than the dominance of the grinding teeth and horns, because in the Eocene titanotheres *Palaeosyops* and *Dolichorhinus* extreme brachycephaly and dolichocephaly appear to be expressed in general changes of proportion which affect all the characters of the skull and teeth and seem to proceed to inadaptive extremes. Similarly, in the comparison above of *Brontops* and *Menodus* we observe that the *Brontops* skulls are increasing in buccal brachycephaly; moreover, that this brachycephalic tendency is manifest in all the measurements of the teeth as compared with those of the dolichocephalic *Menodus*. Thus we can immediately distinguish a grinding tooth of *Menodus* because it is longer than it is broad, in contrast to a grinder of *Brontops*, which is broader than it is long.

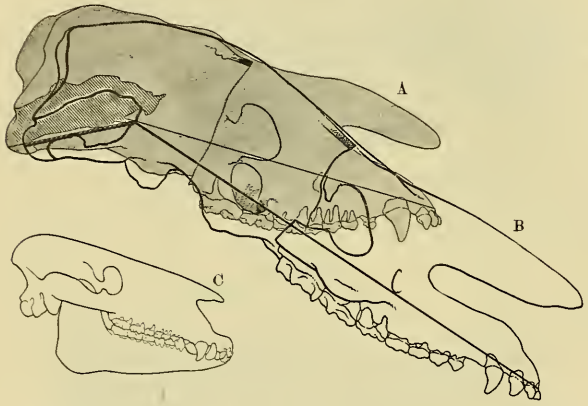


FIGURE 711.—Proportions of skulls of *Palaeosyops*, *Dolichorhinus*, and *Eotitanops*

Midsection of the crania of *Palaeosyops* (A) and *Dolichorhinus* (B), superposed, showing the straight (orthocephalic) and the flexed (cyptocephalic) condition of the faciocranial axes. C, Hypothetic outline of the skull of *Eotitanops*, drawn to the same scale.

Conclusion.—It is not demonstrated that all proportional changes are adaptive; some appear to be relatively inadaptive.

The above is an epitome of the entire evolution of the titanothere skull and of the main tendencies of titanothere skull evolution, which are altogether different from those in any other line of perissodactyls. Each of the Eocene branches, as described in detail in Chapter V, exhibits a distinctive line of cranial and dental evolution in which various extremes of brachycephaly, dolichocephaly, and cyptocephaly evolve more or less rapidly.

RADIATION AND DIVERGENCE IN EOCENE SKULLS

The divergences of the skull from the primitive type in the various Eocene branches are doubtless adaptations to the browsing and grazing habits in different habitats. While in each subfamily branch the 11 main tendencies of titanothere skull evolution, enumerated above, are more or less clearly manifested, there appear certain special generic tendencies distinctive of each line. Some of these changes are prophetic of those that occur in the Oligocene, although they may appear in lines that become extinct in the Eocene and do not lead into the Oligocene genera. They are therefore parallel or convergent and not truly ancestral characters.

EVOLUTION OF THE SKULL IN EOCENE TIME PARTLY PROPHETIC OF THAT IN OLIGOCENE TIME

Abbreviation of the face.—The abbreviation of the muzzle and premaxillary borders in *Palaeosyops* and *Metarhinus*, the abbreviation of the premolar series and elongation of the molar series in all the Eocene phyla is prophetic of Oligocene evolution.

Shifting and reduction of orbits.—The forward shifting and reduction in the size of the orbits occur independently in several of the Eocene phyla, such as *Palaeosyops*, *Manteoceras*, and *Metarhinus*.

Flattening of the cranium.—The spreading of the supratemporal crests, the flattening of the top of the cranium, the closure of the superior cranial and facial sutures occur independently in *Palaeosyops* and *Dolichorhinus*. In the latter the flattening of the cranium proceeds more rapidly than in *Manteoceras*, which is ancestral to certain of the Oligocene titanotheres (*Brontops*). This feature misled Osborn (1908. 318) to suppose that *Dolichorhinus* was an ancestor of the Oligocene genera, an error corrected by Hatcher in his description of *Protitanotherium*.

Massive and slender zygomatic arches.—The massive, wide, arching zygomata of *Palaeosyops* present an independent parallel to those of the basal Oligocene titanotheres. The zygomata of *Telmatotherium* are deep but not spreading; the zygomata of *Manteoceras* are prophetic of the Oligocene *Brontops;* the slender zygomata of *Diplacodon* are analogous to those of *Dolichorhinus*.

INDEPENDENT EVOLUTION OF THE SKULL IN EOCENE TIME NONPROPHETIC OF THAT IN OLIGOCENE TIME

The features of the evolution of the Eocene skull that are quite independent of those of the evolution of the Oligocene skull are principally the following:

Brachycephaly, extreme of, in the Palaeosyopinae.

Dolichocephaly, extreme of, in the Dolichorhininae.

Cyptocephaly, deflected facial region, extreme of, in Dolichorhininae.

Cyptocephaly, upturned facial region, beginnings of, in *Metarhinus*, *Rhadinorhinus* (possibly prophetic of *Megacerops*).

The profound changes in the cranial axis produced by the cyptocephaly of *Dolichorhinus* in comparison with the orthocephaly of *Palaeosyops* are shown in the accompanying diagrams of *Palaeosyops* and *Dolichorhinus*. Gregory was the first to observe the upturned facial region of *Metarhinus* as possibly suggestive of the greatly abbreviated and upturned muzzle of *Megacerops* of the lower Oligocene.

The deflected cranial axis of *Dolichorhinus*, as described in Chapter V, section 4, is connected functionally with its peculiar habits of feeding. These cranial sections are important not only as illustrating the flexure in the cranial axes, but also the great development of the air sinuses of the facial and cranial regions and the relatively small area occupied by the brain.

ZYGOMATIC INDICES

As explained in Chapter V, section 1, the zygomatic index is obtained as follows: Transverse measurement of the zygomatic arches $\times 100 \div$ basilar length of the skull.

The terms brachycephaly and dolichocephaly as used in this monograph are based chiefly on the zygomatic index in the comparison of the total length of the skull with the width across the zygomatic arches, rather than in the comparison of the actual width and length of the cranium proper. From the following table of zygomatic indices it appears that the primitive titanotheres, like other primitive perissodactyls, are dolichocephalic or mesaticephalic. Arranged in descending order according to increase of zygomatic breadth, irrespective of direct descent, the crania are as follows:

Proportions of length and breadth of crania of titanotheres

[Measurements in millimeters]

	Length	Transverse zygomatic	Index	Form of skull
I. Primitive crania:				
Phenacodus wortmani	147	58	32	Dolichocephalic.
Eohippus venticolus	129	53	41	Do.
Hyrachyus sp	263	122	47	Do.
Lophiodon leptorhynchus	360	176	48	Do.
Eotitanops borealis	313	163	51	Do.
II. Progressive dolichocephaly:				
Metarhinus earlei	393	240	61	Mesaticephalic.
Mesatirhinus petersoni (No. 1556)	438	207	47	Dolichocephalic.
Dolichorhinus (No. 1852, ♀)	550	240	43	Dolichocephalic (hyperdolichocephalic)
III. Progressive brachycephaly:				
Manteoceras manteoceras—				
No. 12678	500	[a] 294	59	Mesaticephalic.
No. 2353	[a] 465	277	59	Do.
No. 1569	492	[a] 310	63	Do.
Telmatherium ultimum	500	300	60	Do.
IV. Palaeosyops series:				
Palaeosypos leidyi (No. 1544)	415	310	74	Brachycephalic.
V. Brontops series, progressive brachycephaly:				
Brontops brachycephalus			80	Do.
Brontops dispar			73–87	Do.
Brontops robustus			77–87	Do.
Diploclonus amplus			91	Do.
VI. Brontotherium series, progressive brachycephaly:				
Brontotherium leidyi			66	Dolichocephalic.
Brontotherium hatcheri			74	Mesaticephalic.
Brontotherium gigas			89	Brachycephalic.
Brontotherium platyceras			110	Hyperbrachycephalic.
VII. Menodus series, dolichocephaly, progressive dolichocephaly:				
Allops serotinus			74	Mesaticephalic.
Allops crassicornis			75	Do.
Menodus giganteus			62–70	Dolichocephalic.

[a] Estimated.

It is very important to note that the indices given in the table are zygomatic (buccal) (brachycephalic and dolichocephalic) as distinguished from true cranial (head) indices. The cranium proper is extremely elongate. For example, in *Brontotherium curtum* it extends backward, overhanging the occiput, and forward, overhanging the orbits—in fact, the elongation of the craniofacial summit of the skull is strictly dolichocephalic in the original sense of the word as defined by Retzius.

DIFFERENTIAL EVOLUTION IN SKULL PROPORTIONS IN THE SEVERAL PHYLA OF TITANOTHERES

During the Eocene the dominant tendency in the *Manteoceras* and *Dolichorhinus* phyla was increase in the length of the middle portion of the cranium. This became extreme in *Dolichorhinus*. In *Palaeosyops* and *Limnohyops* the middle portion of the skull was not elongated. During the upper Eocene and lower Oligocene this increase of the middle portion of the skull was surpassed in most phyla by the broadening of the skull, and especially of the zygomatic arches. During lower Oligocene time (Chadron A to C) the three main phyla exhibit approximately equal increments in total cranial length, *Menodus* being only slightly in advance of the others in its percentage increase, as shown in the accompanying diagram (fig. 708).

During the same period the zygomatic breadth, already very great in male skulls of *Brontops brachycephalus*, shows a percentage of increase to the stage of *Brontops robustus* relatively less than in the *Menodus* phylum. The reason *Menodus* during the same geologic period acquired greater zygomatic increase is that the primitive form *Menodus heloceras* was markedly mesaticephalic, lacking the zygomatic expansions entirely, whereas in the largest male, *M. giganteus*, these expansions caused the skull to attain a width index of 55.3. Similarly, the horns appear to increase in length very rapidly in *Menodus*, because of the wide range from the extremely short horns of the lower Oligocene *M. heloceras* to those of the great Field Museum skull of *M. ingens*, in which they have an outside length of 290 millimeters.

In the *Menodus* phylum all the parts except the horns enlarge more uniformly and harmoniously than in the *Brontotherium* phylum. It should be noted that although the total length of the basilar axis of the skull exhibits a similar percentage of increase in the three main phyla, this increase is differently divided between the different parts of the skull. In the *Menodus* phylum, for example, the facial region elongates more rapidly than in the *Brontotherium* phylum, in which the midcranial region elongates rapidly and the facial region is abbreviated.

PALATE AND SHIFTING POSTERIOR NARES

In general, there is a broadening of the palate and gradual shifting backward of the posterior nares. In the more primitive forms the posterior nares opened more anteriorly between the second pair of grinding teeth, m^2. In *Palaeosyops* and *Limnohyops* they frequently open opposite the middle of m^2. In other middle Eocene genera the posterior nares open either opposite the posterior part of m^2 or between m^2 and m^3. In the Oligocene genera the opening of the posterior nares is variable, generally opposite m^3 and sometimes behind m^3.

RUDIMENTS OF HORNS ARISING INDEPENDENTLY IN EOCENE PHYLA

Development of horns and teeth.—The independent origin of the horn rudiments at the junction of the frontal and nasal bones in members of four subfamilies of Eocene titanotheres is one of the most significant facts discovered in the course of the researches for this monograph. In the accompanying table the more or less rapid development of the incipient horns is contrasted with the more or less rapid development of the incipient cusps on the premolar grinding teeth.

As is shown very clearly in Chapter V (pp. 266–267) and Chapter XI (pp. 810–811) the horn rudiments appear geologically early and are very prominent in certain phyla (*Manteoceras, Mesatirhinus*) at a time when in other contemporaneous phyla (*Palaeosyops, Telmatherium*) the skulls are still smooth, entirely hornless. It is only in the late stages of *Palaeosyops* and in geologically late stages of *Telmatherium* that the horn rudiments appear at all. These facts have a double significance, which is fully discussed in Chapter XI (pp. 883–884). First, it would seem that there is a predisposition for the evolution of horns in a certain region of the skull; second, that this predisposition manifests itself not uniformly but in some phyla earlier than in others. There are two deductions from these phenomena:

First, the origin of frontonasal horns is a titanothere family characteristic.

Second, this origin at earlier or later geologic stages is a subfamily or generic characteristic.

Comparison with other perissodactyls.—In the Perissodactyla, as in all other ungulates, there are three more or less concomitant steps in the origin of horns, namely:

1. Psychic predisposition to use the horn as a means of offense and defense, correlated with other offensive and defensive psychoses, linked also with male and female sex glands.

2. Dermal and epidermal thickening, derm pads, and epidermal horny sheaths, protecting layer.

3. Osseous swellings, exostoses, bony swellings beneath the dermal pads or horny sheaths.

Unequal evolution of horns and of premolars in the titanotheres

Horns

	Lambdotherium zone (Wind River B). (500 feet)	Orobippus zone (Bridger A and B). (650 feet)	Uintatherium zone (Bridger C and D). (725 feet)	Eobasileus - Dolichorhinus zone (Washakie B and Uinta A and B). (250 feet)	Diplacodon zone (Uinta C). (600 feet)	Titanotherium zone (Chadron A to C). (180 feet)
Lambdotheriinae	Hornless.					
Eotitanopinae	Hornless.					
Palaeosyopinae		Hornless	"Horns" barely visible and evolving very slowly.			
Telmatheriinae			Horns readily visible.		Horns barely indicated and not developing at all.	
Manteoceratinae (including Protitanotherium).			Horns incipient		Horns expanding rapidly.	
Dolichorhininae		Horns incipient	do	Horns expanding gradually.		
Brontopinae						Horns at first very small, expanding rapidly.
Menodontinae						Do.
Brontotheriinae						Horns at first small, expanding very rapidly.

Premolars

Eotitanopinae	Premolars evolving slowly.					
Palaeosyopinae		Premolars evolving slowly.	Premolars evolving slowly.			
Telmatheriinae			Premolars evolving very slowly.			
Manteoceratinae (including Protitanotherium).			Premolars evolving slowly.	Premolars evolving slowly.	Premolars evolving slowly.	
Dolichorhininae			Premolars evolving more rapidly.	Premolars evolving more rapidly.		
Brontopinae						Premolars evolving slowly.
Menodontinae						Premolars evolving more rapidly.
Brontotheriinae						Premolars evolving very rapidly.

Bony exostoses.—All that we see in fossil skulls are the bony exostoses, or thickenings of the outer bony layer, with expansion of the cancelous bony tissue beneath, as in the horn rudiment of *Palaeosyops* in the accompanying figures.

In the titanotheres, as in the Amblypoda (*Bathyopsis, Coryphodon, Uintatherium*), the bony exostosis expands into a bony horn covered with a thickened dermal pad lacking any evidence of a horny epidermal sheath and certainly without a distinct epidermal horn composed of agglutinated hairs of the rhinoceros type. The bony horns of titanotheres and amblypods become unique among ungulates as great fighting weapons covered with thickened skin pads, rounded, triangular, oval, and finally platelike in form. The absence of horny sheaths is indicated by the absence of the channels for nutrient blood vessels such as surround the bony horn cores of ruminants and of rhinoceroses. The dermal pad of the titanotheres may have been similar originally to the "wart" of the wart hog (*Phacochoerus*), which we may observe as partly protecting the ears when two wart hogs are butting each other.[52] The rounded bony horns of the giraffes are probably degenerate because partly covered with hairs and seldom used.[53]

MODES OF ORIGIN OF THE HORNS OF THE TITANOTHERES

1. Horns originate independently at different periods in four Eocene titanothere phyla.

2. Horns originate invariably above or slightly in front of the orbits, on the line of the nasofrontal suture. The frontal element more or less completely overlaps the underlying nasal elements.

3. Horns apparently have a predisposition or predetermination to originate in this particular region of the face; no evidence of bony horn rudiments is observed in any other part of the skull; the rudiments are invariably continuous with the frontals posteriorly, with the nasals anteriorly.

4. Rudiments of horns are smooth, rounded, not primarily rugose, with no surface indications of channels for large blood vessels. They are totally unlike the vascular horn rudiments of rhinoceroses, such as *Aceratherium incisivum*.

5. The evidence indicates the existence of thickened epidermis rather than of superficial horny sheaths.

6. Horns are equally developed (so far as known) in both sexes in the original Eocene stages.

7. Horns are secondarily more prominently developed in males and less prominently in females.

8. Horns secondarily shift in position on the skull from a point immediately above the orbits to a point more or less above the canines.

9. Horns are originally elongate and oval in form, secondarily of triangular form (*Menodus*), of rounded form (*Megacerops*), of transversely oval form (*Brontotherium*).

10. No evidence is found that the bony horn core develops an independent center of ossification.

From the beginning the titanothere horns are paired and supraorbital in position, as in the Cervidae, Antilopinae, and Giraffidae, among the artiodactyls. and as in *Colonoceras* among the perissodactyls.

PHYLETIC DIVERGENCE IN TIME OF ORIGIN OF HORNS

As is shown in the accompanying diagram (fig. 712), the horns are precocious in origin in the Dolichorhininae—that is, they appear in *Mesatirhinus* of Bridger C as elongate oval swellings overhanging the orbits, at a period when no trace of horn swellings can be observed on the face of the contemporary *Palaeosyops leidyi*. These elongate oval horns of *Mesatirhinus* develop into the prominent oval horns of *Dolichorhinus hyognathus* of Washakie B.

Contemporary with *Mesatirhinus* is the phylum *Manteoceras manteoceras*, the "prophet horn" titanothere, also found near the base of Bridger C. The apparent successor of *Manteoceras*, namely, *Protitanotherium emarginatum* of Uinta C 1, exhibits a horn type which is directly successive to that of *Manteoceras* and similar in form except that it is moved much farther forward over the narial opening.

ACCELERATED DIRECT EVOLUTION OF HORNS IN THE "PROPHET HORN" PHYLUM

In Figure 712 are illustrated five direct stages of evolution, namely, (1) the rudiment of the horn in *Manteoceras* of Bridger C and its shifting forward in *Protitanotherium* of Uinta C 1, (2) its ontogenesis in *Brontops brachycephalus* of Chadron A, (3) its adult form in *Brontops brachycephalus* of Chadron A, (4) its adult form in *Allops marshi* of Chadron B, and (5) its ultimate form in *Brontops robustus* of Chadron C, final stage of evolution.

RETARDED EVOLUTION OF HORNS IN THE PALAEOSYOPINAE AND TELMATHERIINAE

In contrast to the early geologic appearance of the bony horn in the *Eometarhinus, Mesatirhinus, Dolichorhinus*, and *Manteoceras* phyla we observe the extreme retardation of their appearance in the *Palaeosyops* and *Telmatherium* phyla. No horn rudiments are present on the sides of the face in the species of *Limnohyops* and *Palaeosyops* of Bridger C, contemporary with *Manteoceras* and *Mesatirhinus*. As late as Bridger D *Palaeosyops robustus* shows a rounded bony horn rudiment, which becomes quite conspicuous in aged individuals. Skulls of the contemporary *Telmatherium* are unknown, so we can not state positively that *Telmatherium* at this stage lacks the horn rudiment. This rudiment is first directly

[52] Memorandum by W. K. Gregory. See also note on the "horn of *Phacochoerus*" in review of O. C. Marsh's "The 'Brontotheridae,' a new family of fossil mammals." Nature, Jan. 22, 1874, p. 277.

[53] Valuable papers on the genesis of horns are those of Hans Gadow, 1902.1; E. Ray Lankester, 1902.1; J. Ulrich Dürst, 1902.1; and especially Max Weber, 1904.1, p. 23, all cited in full in the bibliography of this chapter.

observed as a very faint sessile, rounded swelling, on the side of the face of a male *Telmatherium ultimum* of Uinta C 1. It would appear from this evidence, which is very strong, if not absolutely conclusive, that whereas in *Manteoceras* and *Dolichorhinus* the rudiments of horns were doubtless present at the time of the deposition of Bridger B and are well developed at the base of Bridger C, they do not appear in *Palaeosyops* until Bridger D, and not certainly in *Telmatherium* until Uinta C 1.

This indirect evidence of the retarded evolution of the horns in certain of the titanotheres (*Palaeosyops, Telmatherium*) and of their acceleration in other Eocene lines (*Eometarhinus, Manteoceras, Mesatirhinus*) is entirely consistent with the retarded or accelerated appearance of other characters, such as the secondary cusps on the premolar teeth, as shown in the above table. It is also consistent with the fact that the Oligocene titanotheres divide into two great branches, namely, the short-horned titanotheres, including the *Menodus* and *Brontops* lines, and the long-horned titanotheres, including the *Megacerops* and *Brontotherium* lines. It is, moreover, consistent with the evidence repeatedly brought forward in this monograph, that the chief difference between phyla consists in the distinctive velocities of their character evolution rather than in the presence or absence of these characters.

FIGURE 712.—Evolution of the frontonasal horn swelling in members of the titanothere subfamilies Manteoceratinae and Brontopinae

A, *Manteoceras manteoceras*, middle Eocene; B, *Protitanotherium emarginatum*, upper Eocene; C, calf stage of Oligocene titanothere (*?Brontops brachycephalus*); D, young titanothere (*Brontops brachycephalus*); E, *Allops marshi*; F, *Brontops robustus*. The horn swelling is at the junction of the nasals and frontals, above the orbits. The frontal swellings grow forward, overlapping the nasals. In the final stage the horn is far in front of the orbits and may be much compressed anteroposteriorly.

DIVERGENCE IN THE FORM OF HORNS OF THE OLIGOCENE TITANOTHERES

The wide divergence in the form of the Oligocene horns is followed in great detail in Chapter VI and need not be recapitulated here. In the short-horned titanotheres there were doubtless very considerable differences in the manner in which the horns were used, both in combats between bulls for the possession of females and as weapons of offense and defense in the combats between the titanotheres and their carnivorous enemies. It is probable that the short-horned titanotheres used a side thrust of the head, while the long-horned types used also a vertical, tossing motion.

CORRELATION (COADAPTATION) OF HORNS WITH CRANIAL AND DENTAL CHARACTERS

There is some reason to believe that the extreme development of the horns in *Brontotherium platyceras* is correlated with extreme development of the buccal plates on the zygomatic arches, which may have served as defensive structures for the side of the skull and face. These gigantic buccal plates are most strongly developed on the skulls having the largest

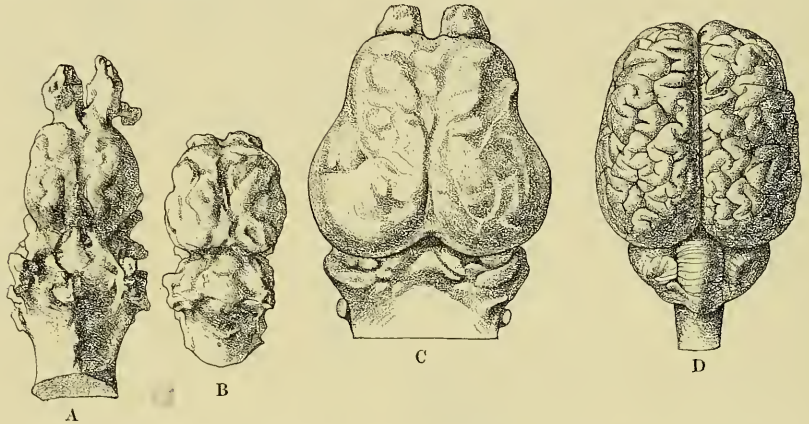


FIGURE 713.—"Brain casts" (intracranial casts) of titanotheres (A, B, C) compared with the brain of a recent rhinoceros (D)

A, *Palaeosyops leidyi*, Am. Mus. 1544; B, *Mesatirhinus petersoni*, Princeton Mus. 10041; C, *Menodus giganteus* (type of *Brontotherium ingens*), after Marsh; D, *Rhinoceros sondaicus*, after Beddard and Treves. In the earliest stage (*Palaeosyops*) the olfactory lobes are relatively large and the cerebral hemispheres are small and do not overlap the cerebellum. The brain cast of *Mesatirhinus* (B) is perhaps somewhat distorted because the cerebra appear to be abnormally wide across the frontal lobes. It is evidently a more progressive type, however, than *Palaeosyops*. In *Menodus giganteus* (C) the cerebral portion appears to be considerably enlarged so as to partly overlap the cerebellum. The anterior lobes, however, are narrower than in the rhinoceros, and the surface was probably much less convoluted. The brain as a whole is also much smaller in proportion to the bulk of the animal.

The connecting crest between the horns is strongly developed in both the short-horned and the long-horned genera (with the exception of *Megacerops*) and is a very conspicuous feature of the evolution of the horns in *Brontotherium*. This connecting crest doubtless served an important mechanical function in withstanding the strain of a lateral thrust. In *Megacerops*, on the contrary, there is little or no connecting crest, indicating the absence of lateral thrust and the use of the horns principally in the tossing up and down motion. In *Brontotherium platyceras* the horns attain supreme development, and in head to head combats the connecting crest of one animal might engage the malar ridges at the side of the horn of the opponent. This general use of the horns for lateral striking and butting as well as for vertical tossing would explain the absence of sharp points at the tips of the horns (as in the ruminants and rhinoceroses) as well as the absence of the pointed horny epidermal sheath, which is the conspicuous offensive and defensive weapon in the rhinoceroses.

horns; and that they are not correlated with the masseter temporalis and other muscles of mastication is proved by the fact that the dental and masticating structures in *Brontotherium* are decidedly inferior to the same organs in the short-horned *Menodus*. These buccal plates are also most strongly developed in the large males and do not appear in the small-horned females. They are thus secondary sexual characters, correlated and coadaptive with the powerful development of the horn, as are also the entire osseous structure of the anterior part of the skull, the inclosure and reduced size of the orbits, the expansion and rugosities of the occiput, the powerful ligamentum nuchae attached to the spines of the anterior dorsal vertebrae—in short, the entire bony and muscular structure of the anterior part of the body.

There is some reason to believe that in the combats between the males for the possession of females the horns attained very high sexual selection value, that there was an incessant selection of the large horns at the expense of the selection of other characters, and that this breeding for large horns may have injuriously affected the evolution of the grinding teeth, which is inferior in *Brontotherium* to the molar-tooth evolution in the short-horned *Menodus*. This problem is discussed in Chapter XI as among the causes of the extinction of the titanotheres.

CORRELATION OF HORNS WITH SEX

Sexual disparity in horn development becomes more marked as we ascend to higher geologic levels. The brontothere females are smaller and wholly different in skull structure from the males; there are also some differences in dental structure which are difficult to comprehend, such as the apparent prominence of the cingulum on the grinding teeth of the females of *Brontotherium* and its absence on the grinding teeth of the males. Even in the male *Brontotherium* the canine teeth are relatively small and inoffensive as weapons, as compared with those of *Menodus*. In the females the canines are greatly reduced in size. This would indicate that, as among the existing horses and cattle, the males stood guard over the herds of titanotheres, protecting the females and the young.

EVOLUTION OF THE BRAIN

The brain cavity of *Mesatirhinus petersoni* and of *Palaeosyops leidyi*, as shown in the intracranial casts (fig. 713), is relatively small. Thus it may be stated that both the Eocene and Oligocene titanotheres—that is, the whole titanothere family—were characterized by a small brain.

We are indebted to Marsh (1884.1) for a discussion of the brain characters of certain Eocene titanotheres and contemporary Eocene ungulates as compared with those of certain related modernized forms; also for excellent illustrations (fig. 714) reproduced herewith. In the titanotheres (*Limnohyops laticeps* and *?Palaeosyops robustus*) we observe again that the brain is relatively smaller than in the contemporary Rhinocerotoidea (*Colonoceras*, *Hyrachyus*, and *Amynodon*). It is also relatively smaller than in the modern *Tapirus*, *Rhinoceros*, and *Equus caballus*.

The disparity in the size of the brain of *Dolichorhinus hyognathus* and of the modern *Equus caballus* is very striking. Inasmuch as the skulls of these two animals are approximately of the same length, they afford an excellent basis of comparison. The ratio of weight of brain to weight of body in all the other large ungulates has been carefully calculated by Max Weber (1897.1) as follows.

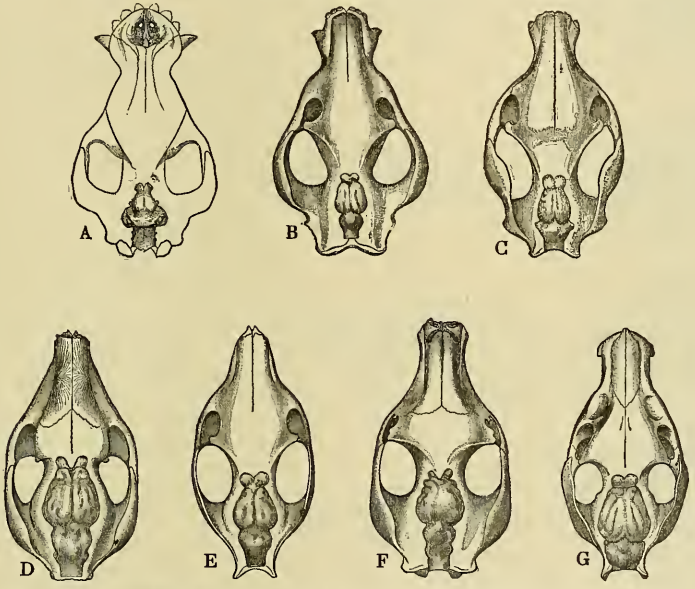


FIGURE 714.—Relative size of brain and skull in titanotheres and other Eocene perissodactyls, an artiodactyl, and an amblypod

After Marsh, 1884.1. Scales various. A, *Coryphodon hamatus*; B, *Limnohyops laticeps*; C, *Palaeosyops robustus*; D, *Colonoceras agrestis*; E, *Hyrachyus bairdianus*; F, *Amynodon advenus*; G, *Eporeodon socialis*

Ratio of weight of brain to weight of body in certain ungulates

	Ratio of brain to body	Percentage of brain to body	Remarks
PERISSODACTYLA			
Tapirus indicus L	1:758	0. 13	
Tapirus americanus L	1:100	1. 00	1 month 4 days old.
Tapirus americanus L	1:947	. 10	Father of above.
Tapirus americanus L	1:140	. 71	Young animal.
Equus zebra L	1:247	. 40	Pretty thin.
PROBOSCIDEA			
Elephas africanus L	1:375	. 25	Lived 10 years.
Elephas indicus L	1:439	. 23	Lived about 25 years.
Elephas indicus L	1:125	. 8	
Elephas indicus L	1:560	. 17	
ARTIODACTYLA			
Cervus elaphus L	1:305	. 33	
Camelopardalis giraffa L	1:392	. 259	2 months old.
Camelopardalis giraffa Schreb.	1:761	. 14	Young.
Camelopardalis giraffa Schreb.	1:777	. 12	Lived 22 years.
Boselaphus tragocamelus Sundw.	1:585	. 17	

The weight of the brains of the early Tertiary ungulates has been considered by Lartet (1868.1), by Bruce (1883.1), by Marsh (1884.1) by Cope, and by Osborn. Cope refers to Lartet's anticipation of Marsh's laws of brain weight, which are as follows:

1. All Tertiary mammals had small brains.

2. The size of the brain gradually increased during the Tertiary period.

3. This increase was confined mainly to the cerebral hemispheres, or higher part of the brain.

4. In some groups the convolutions of the brain have gradually become more complex.

5. In some groups the cerebellum and the olfactory lobes have even diminished in size.

6. There is some evidence that the same general law of brain growth holds good for birds and reptiles from the Cretaceous to the present time.

Marsh enunciated also two additional laws:

1. The brain of a mammal belonging to a vigorous race, fitted for a long survival, is larger than the average brain of that period in the same group.

2. The brain of a mammal of a declining race is smaller than the average brain of its contemporaries of the same group.

DENTAL MECHANISM

The evolution of the upper grinding teeth of the titanotheres, as shown in Figure 718, A–E, proceeds from a purely brachyodont, low-crowned browsing type to a semihypsodont browsing and grazing type. In the earlier stages of evolution (*Eotitanops, Limnohyops, Palaeosyops*) the mode of mastication and the action of the mandible indicate that the principal motion of the jaws was vertical, like that of the omnivorous Carnivora.

In this chopping action of the jaws the pointed incisors, the relatively long, pointed canines, the relatively simple premolars, and the low-crowned molars were correlated with seven changes as follows: (1) The unique feature of the dental evolution is the semihypsodonty (elongation) of the outer side of the crowns of the upper grinding teeth and persistent brachyodonty of the inner side; (2) with this change came the inclination of the wearing plane of the tooth row toward the midline of the tooth, (3) the complication of the premolars by the addition of internal cusps, (4) the ratchet and cog like relations of the upper and lower molars, (5) the changes in the proportions and the arrangement of the masticating muscles, (6) the increasing importance of the oblique shearing effect in the swing of the mandible, together with (7) its pronounced fore-and-aft rocking motion (W. K. Gregory).

These seven coadapted changes resulted in a dental mechanism which combined cutting and triturating functions in a very complex manner and which may have been capable of masticating as wide a range of vegetable food as that of the modern *Rhinoceros* (*Opsiceros*) *bicornis*.

The titanotheres, like other perissodactyls, doubtless had a simple stomach and were incapable of ruminating. Thus the digestive apparatus as a whole was inferior to that of the contemporary camels (*Leptauchenia*), of the numerous oreodonts with crescentic teeth, and of the ancestors of the modern selenodont artiodactyls. Consequently the titanotheres may have derived less nutriment from a similar amount of food to that consumed by the contemporary artiodactyls or may virtually have been debarred from certain kinds of food and certain feeding ranges. The wide and increasing prevalence of ruminant artiodactyls after the decadence of the titanotheres seems to imply a superior digestive apparatus if not a superior dental mechanism, or else a profound change of herbage.

After the extinction of the titanotheres the only successful competitors of the artiodactyls were certain perissodactyls, like the horses and rhinoceroses, especially the great Siberian rhinoceroses (*Elasmotherium*). The Equidae, starting with the same type of molar

teeth as the titanotheres, namely, the bunolophoselenodont, gradually evolved hypsodont molars with highly complex enamel foldings and thereby attained an efficient grinding mechanism capable of triturating the driest and hardest kinds of grasses. (See fig. 718.)

Consequently the imperfect browsing and grazing mechanism of the teeth may have been one of the principal causes of the extinction of the titanotheres. (See Chap. XI.) As more fully discussed in Chapter XI all bunoselenodont Eocene perissodactyls and artiodactyls became extinct in late Eocene or early Oligocene time except only the chalicotheres, which theoretically retreated to the forests and retained the pure browsing habit.

GRADUAL CHANGE OF DIET

The evolution of the grinding teeth in the titanotheres may indicate that all the phyla at first fed upon coarse tubers, roots, and the twigs and leaves of low bushes. The cryptocephalic *Dolichorhinus* may have fared upon the harder and smaller varieties of plants and thus presented a nearer approach to a true grazer. The Oligocene titanotheres probably fared upon larger and coarser varieties of plants, which were plucked up by the powerful prehensile lips. The degeneration or complete loss of the incisor teeth was supplemented by the prehensile lip action. The swollen premolar teeth of the *Protitanotherium* stage, ancestral to *Brontops*, seem adapted for browsing and crushing food rather than for grinding. The pestle and mortar construction of the Oligocene titanothere grinding teeth implies that the food required to be broken and crushed before being ground. The very size of the molars seems to imply very coarse food. The selection of food was apparently never of the harder siliceous varieties sought by the contemporary rhinoceroses and horses, otherwise hypsodont evolution might have been more rapid. The shape of the skull in Oligocene forms seems to imply that the head was not rapidly thrown backward, but that the food was sought near the ground, among the low shrubs. The browsing African rhinoceros *R.* (*Opsiceros*) *bicornis* seems to seek shrubs and browsing food in a country affording admirable opportunity for grazing.

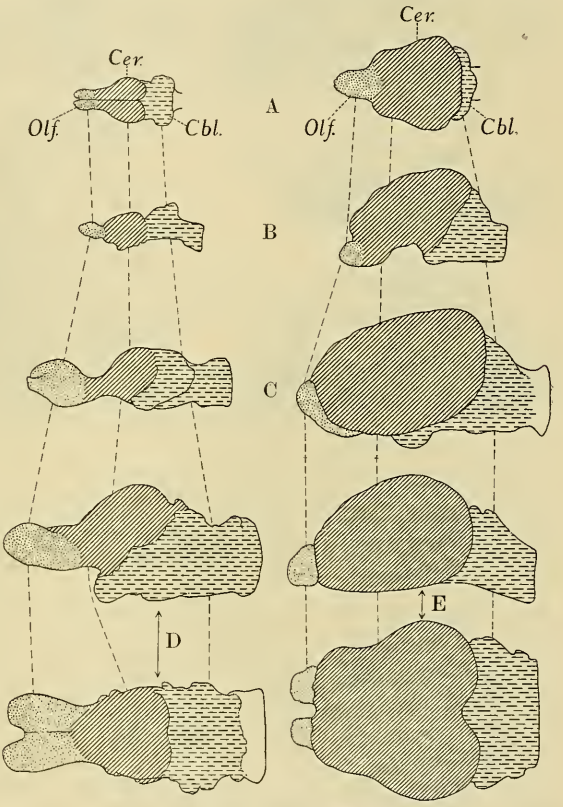


FIGURE 715.—Brain of *Menodus* compared with that of *Rhinoceros* and other quadrupeds

Proportions of brain in archaic (left column) and modernized (right column) mammals of similar size. Dots show olfactory lobes; black lines show cerebral hemispheres; dashes show cerebellum and medulla. All one-fourth natural size. Modified after Osborn, 1910.346. A, *Arctocyon*, Eocene flesh eater; *Canis* (the dog), modern flesh eater. B, *Phenacodus*, Eocene primitive ungulate; *Sus*, the domestic pig. C, *Coryphodon*, Eocene ungulate; *Rhinoceros*, living rhinoceros of same size. D, *Uintatherium*, massive Eocene ungulate E, *Menodus giganteus*, Oligocene titanothere.

HARMONY OF PROPORTIONS OF HEAD AND GRINDING TEETH

A consideration of the proportions of the head and the grinding teeth affords a demonstration of the principle that the evolution of the 11 principal characters of the titanothere skull and dentition is correlated with pervading brachycephaly or dolichocephaly. In the brachycephalic Oligocene titanotheres there is an excess of the transverse over the anteroposterior diameters of the teeth, whereas in the mesaticephalic titanotheres there is an excess of the anteroposterior diameters over the transverse. The facts set forth below should be noted:

1. All the species measured show a considerable degree of fluctuation in the anteroposterior and transverse diameters of all the teeth, a fact which may be due in part to geologic crushing of the rock matrix and in part to actual variability in proportions.

2. There seems to be a higher degree of fluctuation in the diameters of individual teeth than in the total anteroposterior measurements of p^1–m^3, which may indicate compensatory growth.

3. Apparently each species has a typical mean formula and curve for the excess of the transverse over

the anteroposterior measurements in each of the grinding teeth, p^1–m^3.

4. The correlation of the proportions of the individual tooth respectively with the proportions of the molars as compared with the contemporary horses, in which the premolars are rapidly molarized; (4) rare development of mesostyle (median ridge of outer wall) of premolar; (5) feeble development of entoconid of

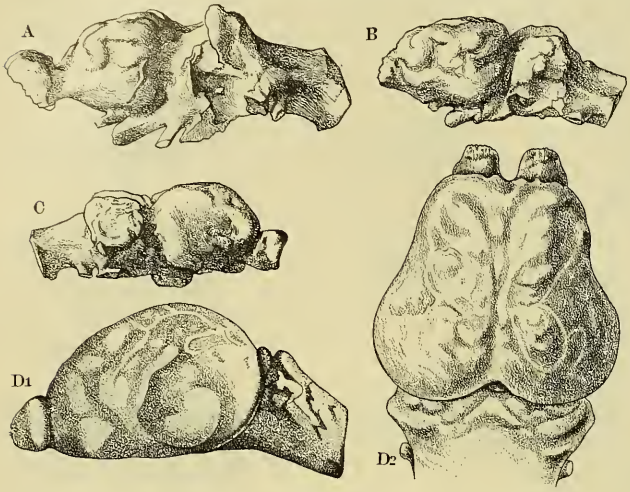


FIGURE 716.—"Brain casts" (intracranial casts) of titanotheres

A, *Palaeosyops leidyi*, Am. Mus. 1544, left side view; B, *Mesatirhinus petersoni*, Princeton Mus. 10041, left side view; C, *Mesatirhinus petersoni*, Am. Mus. 1509, right side view; D_1, *Menodus giganteus* (="*Brontotherium ingens*" of Marsh), left side view, from a cast made under the direction of Professor Marsh; D_2, the same, top view. All one-third natural size. In *Palaeosyops* (A) we see the very large olfactory lobes and the small cerebrum. The brain of *Mesatirhinus* (B, C) appears to be shorter anteroposteriorly.

brachycephalic or dolichocephalic skull is well shown in the curves (fig. 719), the contrast between the dolichocephalic and the brachycephalic forms of grinding teeth being very clear, as well as the progressive broadening of the grinders with the progressive brachycephaly of the *Brontops brachycephalus* and the *B. robustus* phylum.

5. The *Brontops* and *Menodus* curves of the short-horned titanotheres are of the same general type, contrasting with those of the Brontotheriinae.

6. In the Brontotheriinae p^4–m^1 are typically broad; in *Menodus* they are typically narrow.

Although more numerous measurements are needed to make these results absolutely precise or decisive, the general conclusion is sustained that each tooth in each genus and species has its distinctive average and typical proportions.

ARRESTED EVOLUTION IN THE TEETH

The teeth of the titanotheres show the following instances of arrested or retrogressive evolution: (1) Retrogressive evolution of the incisors; (2) retrogressive evolution of the canines in many series; (3) imperfect or retarded molarization of the premolars; (6) hypsodontism of the molars confined to the ectoloph, or outer wall of the crown, a mechanically imperfect evolution; (7) elongation of the molar crowns prevented by the position of the orbits immediately above the grinding teeth.

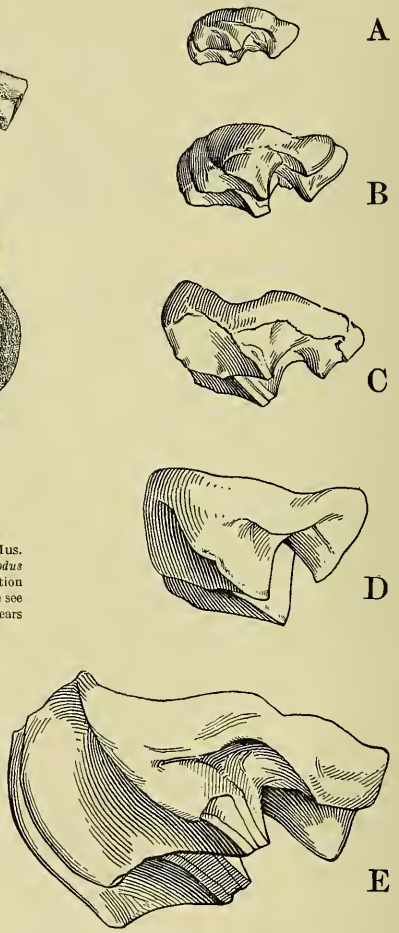


FIGURE 717.—Evolution of the upper molar tooth in titanotheres

Posterior view of a series of left upper molars, showing the gradual deepening of the ectoloph, the persistently low, eonic form of the protocone and hypocone, and the loss of the conules. A, *Eotitanops borealis*, lower Eocene; B, *Limnohyops priscus*, middle Eocene; C, *Manteoceras washakiensis* upper middle Eocene; D, *Telmatherium ultimum* ,upper Eocene; E, *Menodus giganteus*, lower Oligocene.

FORAMINA (NERVE, ARTERIAL) OF THE ATLAS VERTEBRA IN THE TITANOTHERES AND OTHER PERISSODACTYLS

Primitive.—The primitive condition of the atlas (fig. 720, A) is as follows: (1) The first spinal nerve issues laterally, the inferior branch passing down through the "atlantal groove" in front of the pleurapophysis; (2) the same groove also surrounds a branch of the occipital artery; (3) the pleurapophysis is perforated for a short space on the posterior face and under side by the vertebrarterial canal.

Secondary.—Progressive characters of the atlas in the Perissodactyla are:

1. The first character is the bridging over of the atlantal notch or groove by the pleurapophysis, this resulting in a condition like that seen in *Tapirus* (fig. 720, C). This bridging over of the atlantal groove is rare in Eocene titanotheres, although it is represented in a supposed *Palaeosyops* atlas figured by Earle (1892.1, pl. 13, fig. 29; see bibliography, p. 698); is not present in Oligocene titanotheres.

2. The loss of the vertebrarterial canal on the lower side of the pleurapophysis. It is a striking peculiarity that some of the Oligocene titanotheres lose this canal entirely. In some cases this loss seems to be preceded by the constriction of the canal, as in the atlas of *Telmatherium ultimum;* in others the vertebral artery apparently evaded the canal entirely and passed directly from the axis beneath the pleurapophysis to its possible junction with the occipital artery (fig. 720, B).

Titanotheres.—The titanothere family characters of the atlas vertebra are as follows:

1. Atlantal foramen open or bridged. The first cervical nerve and a branch of the occipital artery deeply indent or groove the anterior borders of the pleurapophysis; in certain forms (*Manteoceras, Limnohyops, ?Palaeosyops, Dolichorhinus,* see accompanying fig. 720) the groove is not bridged over by bone; in other forms (*Palaeosyops* as figured by Earle, op. cit., figs. 28, 29) the groove is bridged over. In the Oligocene genera the groove is open in certain forms (*Brontops robustus;* see Pl. CXCV of this memoir), and bridged in others. This bridging is partly an age character. In all modern tapirs, horses, and rhinoceroses the atlantal groove is bridged over.

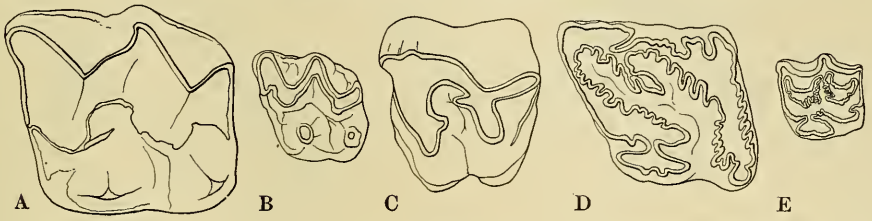


FIGURE 718.—Pattern of an upper molar of five perissodactyls, showing the widely different extent of the enamel edges and surfaces

A, *Menodus giganteus,* an Oligocene titanothere; B, *Palaeosyops robustus,* a middle Eocene titanothere; C, *Teleoceras,* a Miocene rhinoceros; D, *Elasmotherium,* a very highly specialized Pleistocene rhinoceros; E, *Equus,* a modern horse. Scale uniform. In A and B the total length of the enamel edges is relatively short; in D and E it is excessively long. The more simple molar crowns, with short enamel edges, are adapted to crushing coarse vegetation; the more complex crowns, with greatly elongated enamel edges, are adapted to the trituration of hard siliceous shrubs and grasses.

2. The vertebrarterial canal pierces the inferior lamella of the pleurapophysis in the Eocene Brontotheriidae as in the modern Tapiridae, whereas in the modern Equidae and Rhinocerotidae it enters the superior face of the lamella. A distinctive progressive feature in certain of the Brontotheriidae, first seen in the upper Uinta forms *Telmatherium ultimum* and *Protitanotherium,* is that the vertebrarterial canal tends to close or become obliterated

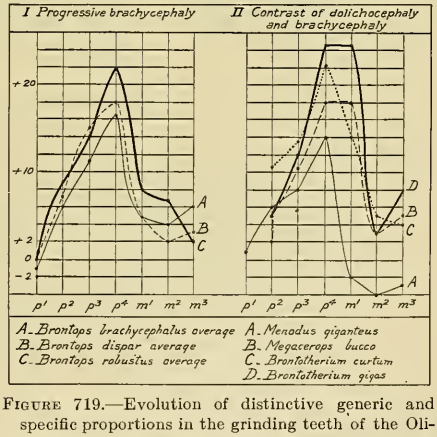


FIGURE 719.—Evolution of distinctive generic and specific proportions in the grinding teeth of the Oligocene titanotheres

I, Increasing excess of transverse over anteroposterior diameters and progressive brachycephalic tendency in the *Brontops* phylum; also illustrating the mean formulae for three species of *Brontops.* II, Contrast between the extreme brachycephalic tendency in *Brontotherium* and *Megacerops* with the extreme dolichocephalic tendency in *Menodus giganteus.* In *Brontotherium* p^1–m^1 are exceptionally broad; in *Menodus* p^1–m^1 are exceptionally narrow.

entirely, causing the vertebral artery to pass beneath the pleurapophysis without perforating it. Thus in certain Oligocene titanotheres the vertebrarterial canal is reduced or wanting.

By comparison with the tapirs, rhinoceroses, paleotheres, horses, and other perissodactyls we have found (1) that the locomotor skeleton of the titanotheres exhibits certain distinctive titanothere family features; (2) that in its cursorial, mediportal, and graviportal adaptations it closely parallels the perissodactyls of other families, living and extinct; (3) that through divergence from each other in modes of feeding and locomotion there evolved a great variety of titanotheres, adapted to the varied feeding and soil conditions of the mountain-basin and plains regions. Our inquiry has been directed to three determinations—proportions of the feet and limbs; proportions of the head and body of the animal as a whole; weight of the animal as a whole.

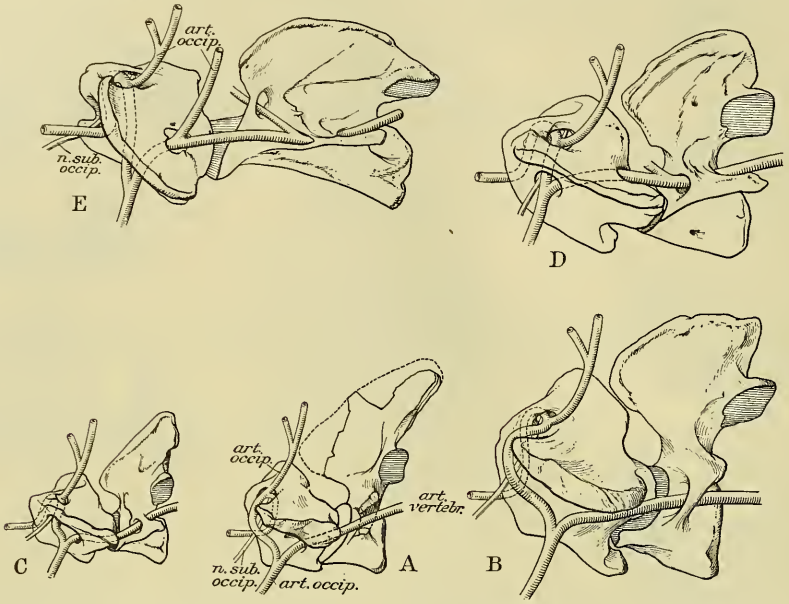


FIGURE 720.—Atlas and axis of titanotheres and other perissodactyls, showing probable course of the arteries through atlas

Based on comparison with the horse and rhinoceros, Gregory and Christman, 1920. One-fourth natural size.

A, *Manteoceras*, Am. Mus. 12204. The transverse process of the atlas was pierced posteriorly by the vertebral artery, which probably then united (below the transverse process) with the ascending trunk of the occipital artery, which in turn ran dorsally and passed through the atlanta groove and foramen, again turning sharply downward and finally turning forward and entering the cranial cavity along the floor of the spinal canal. The suboccipital nerve (N. cervicalis I) passed outward and downward through the atlantal foramen. These are the conditions in typical placental mammals, and the positions of the foramina and grooves of the atlas indicate that they were retained by Eocene titanotheres from *Eotitanops* onward.

B, *Brontotherium leidyi*, Carnegie Mus. 114. The vertebral artery did not pierce the transverse process of the atlas posteriorly but probably passed immediately below it. The transition from the primitive conditions shown in A apparently took place in *Eotitanotherium osborni*, of the upper Eocene, for Mr. Peterson records the fact that in the type atlas the base of the transverse process was pierced by a small foramen, whereas in the paratype of the same species there is no evidence of the foramen.

C, *Tapirus americanus*. The atlantal groove is bridged over by the anterior border of the transverse process.

D, *Opsiceros bicornis*, black rhinoceros. The vertebral artery enters the base of the transverse process on the upper surface, but the course of the tunnel is otherwise normal. The atlantal groove is bridged, as in C.

E, *Equus caballus*. The vertebral artery pierces the transverse process on its upper surface and then joins the occipital artery. The atlantal groove is bridged.

PROGRESSIVE ADAPTATIONS OF THE PECTORAL AND PELVIC ARCHES, THE LIMBS, AND THE FEET OF THE TITANOTHERES

From the chief adaptations to speed and weight in the limbs of the larger ungulates (Chap. VIII, sec. 3) we may deduce from the bony limb structure of the titanotheres some knowledge of their relative size—that is, their height and weight combined—as well as of the speed and general mode of locomotion of the different Eocene and Oligocene forms.

ANCESTRAL TITANOTHERES SUBCURSORIAL

The limbs of *Lambdotherium* are unquestionably of primitive cursorial type, and those of *Eotitanops* are of subcursorial type, but these genera point alike to a more primitive cursorial ancestry. These facts appear to warrant the generalization that all the early titanotheres (see pp. 733, 736) were small, light, cursorial animals, and that the mediportal and graviportal forms were secondary, a generalization that is indicated also by the skull and dentition.

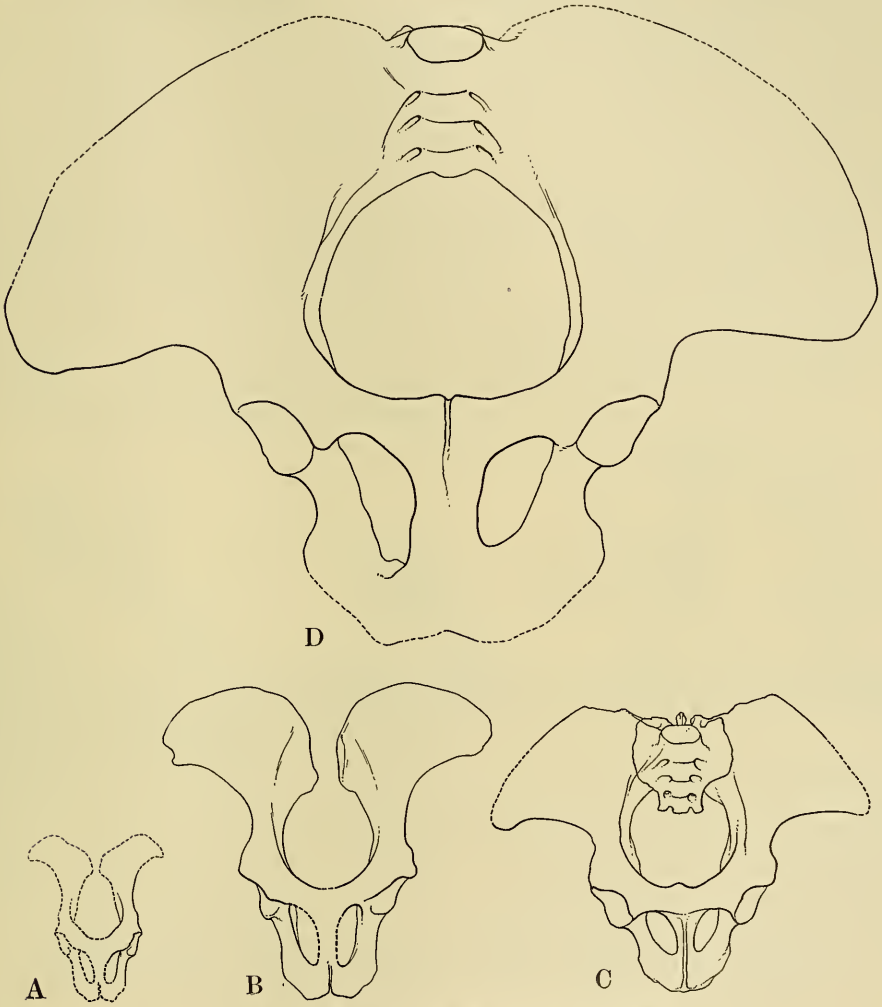


FIGURE 721.—Evolution of the pelvis in the titanotheres

Four progressive stages of adaptation: A, The subcursorial *Eotitanops borealis*, Am. Mus. 14887, lower Eocene; B, the mediportal *Palaeosyops major*, Am. Mus. 13116, middle Eocene (lower Bridger); C, the subgraviportal *Manteoceras manteoceras*, Am. Mus. 2358, upper Eocene of Washakie Basin; D, the graviportal *Brontotherium gigas*, Am. Mus. 492, lower Oligocene. All one-eighth natural size. In the first stage, *Eotitanops*, the pelvis is long and narrow, as in other primitive perissodactyls. In succeeding stages the gluteal blade of the ilium becomes transversely expanded, so that in the final stage the transverse diameter across the ilia greatly exceeds the anteroposterior diameter. All this constitutes an adaptation to progressively graviportal habits, as in the elephants.

A significant fact, to which W. K. Gregory first called attention and which is commented on early in this chapter, is that of all the early Eocene perissodactyls known, the oldest representatives of three

families—the Equidae, Helaletinae (Lophiodontidae), and Hyracodontidae—are cursorial or subcursorial. This prevalence of primitive cursorial types points to the hypothesis that the most primitive titanotheres, like the other Perissodactyla, the Artiodactyla, and the Condylarthra, were largely (if not wholly) cursorial or subcursorial animals, from which the larger mediportal and graviportal titanotheres evolved. This hypothesis, as Gregory (1910.1) points out, is sustained by the carpal and tarsal structure in most of the early perissodactyls and by what is known of *Lambdotherium*. In accordance with the principle of survival through natural selection, the early perissodactyls, being of diminutive size and without defensive weapons of any kind, would survive by adopting a relatively swift gait to escape their enemies.

In the remote ancestral perissodactyl types, including the titanotheres, so far as known, the arches and limbs were slender, the manus and pes were relatively elongate, and the carpals and tarsals were high and narrow.

The details of structure of the limbs of the lower Eocene *Lambdotherium* and of *Eotitanops* are described on pages 590–598.

THE TITANOTHERE PES

The early titanotheres show the following characters in common with other early perissodactyls: (1) Tridactyl, no trace of D. I or D. V; (2) digits relatively elongate, laterally compressed; (3) astragalus with elongate neck and three entirely separate astragalocalcaneal facets (Osborn, 1890.51), the ectal (e), the vertically elongated "sustentaculars," and the "inferior" (i), the last usually small and separate; (4) astragalocuboidal facet narrowing to a point anteriorly, whereas in the middle Eocene titanotheres it is progressively broad; (5) calcaneofibular facet, or pit, functional in titanotheres and equines.

The proportions and facets of the pes of titanotheres must be interpreted by considering the common ancestry of the titanotheres with the other perissodactyls and the special submediportal divergence of the pes. Thus, in the evolution of the feet of the several forms of the perissodactyls the contrasts are as follows:

Forms of the elements of the pes in three types of perissodactyls

Element	Cursorial	Submediportal	Graviportal
Digits	Elongated or stilted	Relatively short, expanded	Broad and stout.
Tarsal elements	Narrow and elevated	Broader	Extremely broad.
Sustentaculum astragali	Contracted and elevated	Spreading	Spreading and continuous.
Tuber calcis	Rounded and slender	Expanding	Massive.

Judging by these tests the gradations as to weight and speed among these lower Eocene titanotheres, as compared with contemporary perissodactyls, were as follows:

Ancestral titanothere *Eotitanops*, larger, least cursorial.
Cursorial titanothere *Lambdotherium*, smaller, transitional.
Cursorial lophiodont *Heptodon*, more slender and cursorial.
Cursorial horse *Eohippus*, most slender and cursorial.

Thus all the elements of the pes of *Eotitanops* may be distinguished in all their facets and other parts as broader and more expanded laterally than those of *Heptodon* and *Eohippus*, which are compressed laterally and expanded anteroposteriorly.

PROGRESSIVE STAGES OF THE MANUS

A comparison of the evolution of the manus in the ascending series of titanotheres, as illustrated in Figures 722–723, shows a complete transition from the cursorial through the mediportal to the graviportal type, modified throughout by certain peculiar titanothere family tendencies, namely, (1) increase in size; (2) secondary enlargement of D. V, which finally nearly equals D. II in size, a titanothere peculiarity; (3) secondary substitution of paraxonic for mesaxonic condition, a titanothere peculiarity; (4) flattening of all the small bones of the carpus; (5) abbreviation of all the phalanges, especially of the terminal phalanges supporting the horn sheaths; (6) progressive expansion of the lunar upon the magnum in adaptation to tetradactyly, to the paraxonic condition, and to the progressive graviportal condition; (7) gradual atrophy of the trapezium, which becomes vestigial.

THE TITANOTHERE MAGNUM

The progressive stages in the evolution of a single bone, the magnum, demonstrate that each bone of the carpus passes through a complete succession of stages from the cursorial to the graviportal type; that each bone reflects what it is correlated and coadapted with, namely, the bodily history of the entire organism; that each bone if examined with sufficient thoroughness and minuteness would reveal generic and probably specific characters capable of definition.

The magnum, as the central bone of the carpus, in the course of adaptation from the cursorial condition in *Eotitanops* to the extreme graviportal condition in *Brontotherium*, changes its diameters completely, evolving from a high, narrow form (*Eotitanops*) into a broad, low, flattened form (*Brontotherium*). It has

six facets, as follows: Magnum-trapezoid, magnum-scaphoid, magnum-lunar, magnum-unciform, magnum-Mtc III, magnum-Mtc II. The most significant change is that in the passage from the vertical to the

EVOLUTION OF THE ASTRAGALUS

The astragalus of the tarsus displays similarly a complete transformation in its facets in passing from the cursorial through the mediportal to the gravi-

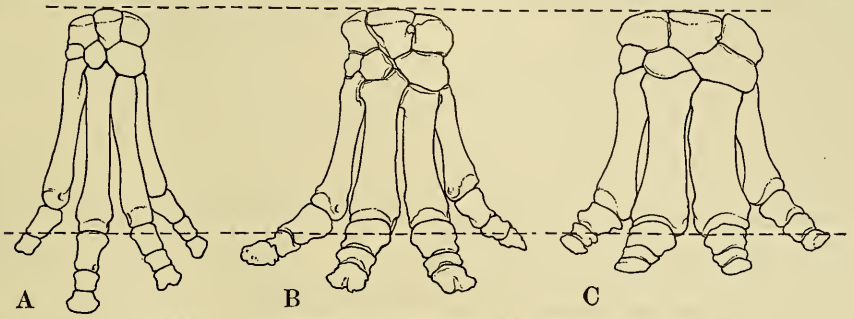


FIGURE 722.—Three stages in the evolution of the manus in titanotheres

A, Subcursorial (*Eotitanops*); B, mediportal (*Limnohyops*); C, graviportal (*Brontotherium*). Not drawn to scale. In all three figures the height from the top of the lunar to the bottom of the third metacarpal is arbitrarily made equal. In this way the progressive relative widening of the metacarpals, the shortening of the phalanges, and the great widening of the carpals are revealed.

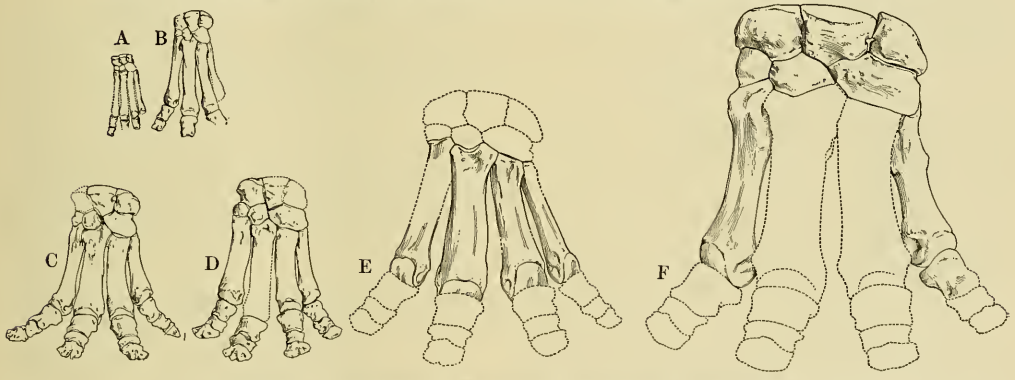


FIGURE 723.—Six stages in the evolution of the manus in titanotheres

A, *Lambdotherium*, lower Eocene; B, *Eotitanops*, lower Eocene; C, *Limnohyops monoconus*, middle Eocene; D, *Monteoceras manteoceras*, middle Eocene; E, "*Diplacodon*," upper Eocene; F, *Brontotherium*, lower Oligocene. The earlier members of this series retain the more primitive perissodactyl cursorial pattern of the manus. The carpus is of the interlocking, displaced type, and the third digit is predominant. In the mediportal and graviportal members the whole manus becomes very wide, digits III and IV become subequal, and the lunar and magnum broaden.

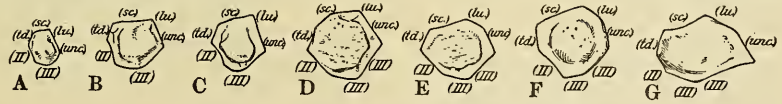


FIGURE 724.—Evolution of the magnum in titanotheres

Cursorial, mediportal, and graviportal types. This series shows the progressive widening of the magnum (the increase of the horizontal compared with the vertical diameter) in correlation with the widening of the whole foot, a graviportal adaptation. The facets for scaphoid, lunar, and Mtc III are greatly widened. A, *Eotitanops borealis*, Am. Mus. 296, lower Eocene; B, *Mesatirhinus petersoni*, Princeton Mus. 10013, middle Eocene; C, *Manteoceras manteoceras*, Am. Mus. 12204, middle Eocene; D, *Palaeosyops copei* (?referred), Am. Mus. 12205, middle Eocene; E, *Palaeosyops robustus*, Am. Mus. 1581, middle Eocene; F, *Dolichorhinus longiceps*?, Carnegie Mus. 2865, upper Eocene; G, *Brontotherium gigas*, Am. Mus. 1443, lower Oligocene.

lateral expansion, the magnum passes beneath the lunar (as described above in this chapter) and the lunar also spreads over the upper surface of the magnum. Thus, as was first pointed out by Osborn (1890.51, sec. 4), the growth of the magnum and lunar is reciprocal.

portal type, in the course of which it parallels other perissodactyls in their similar transformation, while it also displays certain peculiar titanothere family features. In the diagram of Figure 701 we observe a series of stages corresponding with those observed in the manus and in the magnum, namely, the trans-

formation from a small, high, narrow type of astragalus, adapted to the cursorial foot of *Lambdotherium*, through the broadening mediportal stages exhibited in *Limnohyops* and *Manteoceras*, into the subgraviportal *Protitanotherium* and the massive graviportal *Brontotherium*.

The following five detailed changes are evolved, all of which are more or less closely paralleled in other lines of ungulates in the passage from the cursorial to the graviportal condition: (1) A maximum vertical diameter (height and width index) is replaced by a maximum horizontal diameter (height and width index); (2) the neck, or cervix, is relatively abbreviated; (3) the astragalocuboidal facet is greatly broadened, a process analogous to the extension of the lunar upon the magnum in the manus; (4) the ectosustentacular and inferior astragalocalcaneal facets are separated; (5) the astragalocalcaneal facet is vertically elongated in *Lambdotherium* and becomes rounded in *Brontotherium*.

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CHAPTER XI

CAUSES OF THE EVOLUTION AND EXTINCTION OF THE TITANOTHERES

In section 1 of this chapter two chief processes of evolution are traced in detail in the long history of the titanotheres—the evolution of new proportions (allometrons) and the rise and evolution of new characters (rectigradations). Both processes proceed along direct, continuous, orthogenetic lines, and both are of great biologic and sytematic significance.

In section 2 the causes of the extinction of the titanotheres and other quadrupeds are considered in the light of Darwin's theory of natural selection.

FIGURE 725.—Restorations of *Eotitanops borealis* (right) and *Brontotherium platyceras* (left): the earliest and the latest stage in the evolution of the titanotheres

SECTION 1. MODES AND CAUSES OF THE ORIGIN AND EVOLUTION OF NEW ADAPTIVE CHARACTERS (RECTIGRADATIONS) AND NEW PROPORTIONS (ALLOMETRONS) IN OLD CHARACTERS

DISTINCTIONS BETWEEN MODES AND CAUSES

Evolution of the heredity germ.—A host of new characters and of new proportions in old characters separate *Brontotherium* from *Eotitanops*, and all these characters are germinal, hereditary. The problem here considered is, How and why did the heredity germ of *Eotitanops* evolve into that of *Brontotherium?* "How" is a question of the modes of evolution; this question we have in large part answered. "Why" is a question of the causes of evolution; this question we have answered only in small part. Let us examine four points of distinction between "modes" and "causes."

Biocharacters (single characters).—Throughout the research made for this monograph far more attention has been devoted to a study of the modes of evolution of "single characters," which we may term "biocharacters," than to artificial groupings into "mutations," "species," and "genera." The titanotheres exhibit with extraordinary clearness the origin, evolution, survival, and elimination of biocharacters. Detailed observations extending over nineteen years are not without reward. The long history disclosed by hundreds, even thousands, of titanothere biocharacters in the teeth and skeleton throws light upon three of the still unsolved great problems of the modes of evolution, namely:

Modes of origin of new adaptive biocharacters = rectigradations.

Modes of origin of new proportions in biocharacters = allometrons.

Modes of survival and elimination of biocharacters = selection.

Distinctions to be noted.—We must keep constantly in mind the distinction between the comparatively well understood modes of evolution, which follow certain well-established principles that apply to all living beings, and the still mysterious causes of evolution, which follow principles yet to be discovered. The

so-called "laws of evolution" thus far discovered relate chiefly to modes and in but small degree to causes. Nevertheless the observation of the modes of evolution exemplified in the titanotheres and other animals bears adversely or favorably upon one or another of the various theories that have been advanced as to the causes of evolution.

The study of evolution may be divided into a study of facts more or less fully ascertained by comparative studies of the invertebrates and vertebrates through the sciences of zoology, comparative anatomy, experimental zoology, genetics, invertebrate and vertebrate paleontology, and a consideration of hypotheses as to the causes of evolution, such as those presented by Buffon, Lamarck, Spencer, Darwin, Wallace, Cope, Weismann, De Vries, Osborn, Loeb, Morgan, and other naturalists, experimentalists, and biochemists.

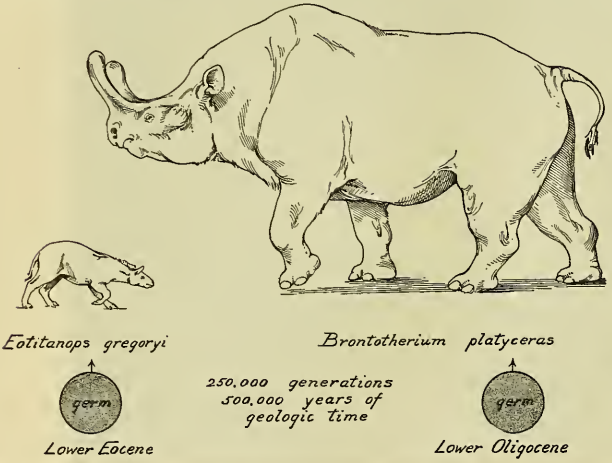


FIGURE 726.—Relations of the heredity germ of *Eotitanops gregoryi* to that of *Brontotherium platyceras*

Animals are one-fiftieth natural size.

SPECULATION AS TO THE CAUSES OF EVOLUTION

Many vertebrate paleontologists have contributed to our knowledge of the modes of evolution of the extinct vertebrates, notably Cuvier, Owen, Huxley, Gaudry, Leidy, Cope, Marsh, Kowalevsky, Williston, Scott, Osborn, Depéret, Smith Woodward, Andrews, Dollo, Abel, Merriam, Matthew, and Gregory. Only a few—among them Buffon, Lamarck, St. Hilaire, Spencer, Cope, and Osborn—have attempted even to speculate upon the causes of evolution of the vertebrates. Lamarck, Spencer, and Cope are the principal contributors to the Lamarckian hypothesis of inheritance by the germ of the mechanical modifications of the body, and to the related hypotheses of kinetogenesis, of growth force, and of "bathmism," all dependent upon the supposed inheritance by offspring of the influences of bodily characters acquired through the habits of the parents. Scott has pointed out the very important distinction observable in vertebrates between the principle underlying the "mutations" of Waagen and the "variations" and "variability" of Darwin. Osborn has developed a hypothesis for the principle of rectigradation as of potential homology, and has proposed a theory of tetraplasy in growth and development and of tetrakinesis in evolution, the latter based upon conceptions of energy.

DISTINCTION BETWEEN INVISIBLE GERM EVOLUTION AND VISIBLE BODILY EVOLUTION IN THE TITANOTHERES

In observing the modes of evolution, and still more in speculating upon the causes of evolution, it is necessary to keep in mind always the sharp distinction between the invisible evolution of the germ and the visible evolution of the body. The germ contains the heredity units of all the predispositions and potentialities of body form and function, units figuratively known as "factors," "determiners," or "genes," which may control the development into normal visible body form only under the favorable influence of normal habit and environment. The body of the titanothere, on the other hand, is the component of the fourfold (tetraplastic) influence of the animal's germ cells, of its habits, of its physical environment, and of its life environment.

Germ evolution represents incessant changes in heredity; bodily development represents four factors—heredity, physical environment, life environment, and habit (ontogeny). With this distinction clearly in mind, if we contrast the beginning and the end of titanothere bodily evolution we observe that the heredity germ of *Brontotherium platyceras* was very different from that of its remote ancestor *Eotitanops borealis*. Perhaps 500,000 years of geologic time separated *Eotitanops* from *Brontotherium*. Allowing one generation on the average for every two years, two hundred and fifty thousand generations of titanotheres separated *Eotitanops borealis* from *Brontotherium platyceras*.

Since the adult *Brontotherium* differs very widely from the adult *Eotitanops* in all its visible biocharacters it certainly reflects a great number of new or transformed germinal predispositions. For example, say the germ of *Eotitanops* contains 300,000 predispositions, that of *Brontotherium* contains perhaps 500,000. How did the predispositions of these 200,000 new or transformed biocharacters enter the heredity germ? Whatever the number, certainly the heredity germ of *Brontotherium* was in its predispositions and potentialities vastly different, more

complex, and more imposing than that of *Eotitanops*. How was the heredity germ thus enriched; how did all these new predispositions of character, new qualities, and new potentialities enter the germinal substance? We know from comparative embryology and heredity that there was a direct continuity between the heredity germ of *Eotitanops* and that of *Brontotherium* (fig. 727); also that the germinal predispositions and potentialities were handed down continuously, and that while the germ flowed outward into the form and functions of the body there is little or no Lamarckian evidence that the modifications of the form and functions of the body flowed inward into the germ of the succeeding generation—that is, there is little evidence in titanothere evolution for the Lamarck-Cope-Spencer doctrine of kinetogenesis, or inheritance of bodily modifications.

PRINCIPLES OF TETRAPLASY IN INDIVIDUAL DEVELOPMENT; ONTOGENY

One contrast between the causes of individual bodily development (ontogeny) and those of racial (germinal) evolution (phylogeny) is that the former are observedly tetraplastic, the latter are hypothetically so—that is, the influences of the body and of the environment on the germ are as yet hypothetic.

We may now speak briefly of the fundamental tetraplastic principles (Osborn, 1908.308) of individual development, which will be more fully explained farther on in this chapter (pp. 835–838).

To distinguish clearly the fact that every visible titanothere is the component of four physico-chemico-mechanical influences and is continually subject to selection in competition with other titanotheres, it is necessary to keep in view the following scheme:

Tetraplasy: Inseparable action, reaction, and interaction of four complexes of causes, together with natural selection, on development

1. *Titanothere germ evolution*

Genesis of new germinal predispositions and potentialities, giving rise to new biocharacters, to new changes of form and proportion, continuous and discontinuous, to the hastening or retarding of existing biocharacters in development and evolution, to new predispositions to correlation and compensation of biocharacters, which give rise to new germinal "mutations," "ascending mutations," "rectigradations," "allometrons," etc.

2. *Ontogeny*

The development of the body (soma) of the individual titanothere; influence of habit, use, and disuse upon the germinal predispositions of function and structure; genesis of new somatic modifications, of new somatic characters, of somatic changes of form and proportion, of somatic hastening and retarding of biocharacters, of somatic correlation and compensation of biocharacters that may give rise to allometrons, "ontogenetic variations," "ontogenetic species," etc.

3. *Physical environment*

Geographic environment (earth, air, water, temperature, etc.). If highly favorable, environment intensifies and overdevelops certain germinal predispositions, potentialities, tendencies of every biocharacter in the soma; if unfavorable, it dwarfs, arrests, inhibits, or actually suppresses them. Environmental influence on the appearance of new somatic biocharacters, on changing form and proportions of somatic biocharacters, on the hastening and retarding of the individual development of somatic biocharacters, on the correlation and compensation of somatic biocharacters, concluding in extreme cases in the formation of "environmental species," "climatic variations," "geographic species," "geographic variations," "geographic varieties," etc.

4. *Life environment*

Plant and animal complex—flora and fauna, biota surrounding the organisms. Influence of all the competing organisms on the predispositions and potentialities of the titanothere germ, chemico-physical influence of different kinds of food, mechanical influence of food, and complex of the combined influence of food and of habit on ontogeny. Competition with titanotheres of the same and of other varieties in the search for food.

5. *"Natural selection" of Darwin; "survival of the fittest" of Spencer*

Effect of competition with members of the same and other species on all the functions and structures developed from the predispositions and potentialities of the germ as influenced by environment and ontogeny, including the direct action of selection on all biocharacters that have survival value, resulting in the selection of the germinal predispositions from which they spring, according to the germinal selection theory of Weissman, which includes, in part, the "organic selection" or "coincident selection" of Osborn, Morgan, and Baldwin.

Thus four physico-chemical and mechanical factors interoperate with selection according to Osborn's principle of tetraplasy. Every stage in the development of each titanothere, from youth to old age, was thus tetraplastic; every visible biocharacter was the resultant of these fourfold factors. Natural selection is not in the same sense a factor or a force; it is an arbiter between the individual titanotheres as molded by hereditary predisposition, by life habit, and by the physical and the life environment. These are the observed modes of titanothere development. The hypothetic action of these modes of evolution is considered on pages 835–838 in the discussion of tetrakinesis.

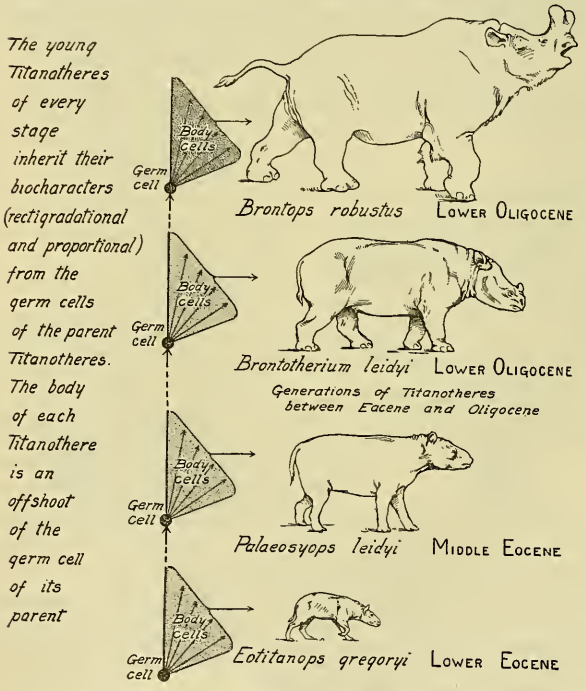


FIGURE 727.—Continuity of the heredity germ from *Eotitanops* to *Brontops*, according to Weismann's theory of the "continuity of the germ plasm"

PRINCIPLES OF SINGLE CHARACTER (BIOCHARACTER) EVOLUTION

In the titanotheres, as in other animals, the body is composed of a large number of correlated single elements, characters, or biocharacters, each of which has its more or less independent origin, development, transformation, rise, or decline. These biocharacters, which are separable in individual development and in evolution, are separable also in heredity, a fact known by comparing them with similar biocharacters in the hybridization of living animals like the horse, a perissodactyl remotely related to the titanotheres.

A biocharacter (Osborn, 1917.460) is any single part or function of an animal which is known to have separate origin, growth, evolution, ontogenetic or individual rate (velocity) of development, phylogenetic or racial rate (velocity) of evolution, and a presumable separability in the heredity of the germ. A biocharacter partly corresponds to the "unit character" of Mendelism.

Examples of biocharacters of the titanotheres are the single cusps of the grinding teeth, the single horns on the skull, the old and new proportions of the skull and of the limb bones. The term is thus very elastic, because it refers to larger and smaller character groups which evolve and are heritable together more or less as units. The term is both bodily (somatic) and germinal in application, for each visible biocharacter may have a number of genes or determiners in the heredity germ.

Four chief kinds of biocharacters in the teeth and skeleton are common to the titanotheres and other mammals of the paleontologic series, some of which correspond with the heritable variations and fluctuations of Darwin, as shown below.

1. *Saltation biocharacters.*—Numerical saltations; suddenly appearing complete additional parts; multiplication of parts, rarely adaptive (such as supernumerary vertebrae, ribs, digits, teeth), duplication of existing parts (such as duplication of dental cusps, duplication of the tips of the horns). Similar to certain numerical and "meristic" variations in other animals (such as hyperdactyly, hyperphalangy). These suddenly appearing new characters are complete structures; they are all germinal in origin and are usually abnormal.

2. *Quantitative variations, fluctuations.*—Variations (Darwin), chance variations, minor saltations, minor discontinuities (Bateson), minor plus and minus variations; the quantitative and intensive fluctuation of characters around a mean (Quetelet), in a single curve, or in a double curve where two separate evolutionary phyla are hybridized. These minute accidental characters include in part the "mutations of De Vries," which take accidental, chance, or variable directions, as distinguished from the rectigradations of Osborn. All are germinal in origin and are supposed by Darwin to form the chief material out of which selection builds up adaptations through gradual accumulation in one direction.

3. *Rectigradation biocharacters.*—Rectigradations of Osborn; new characters developing adaptively, orthogenetically, from the beginning, arising from minute and inconspicuous rudiments (such as new units of structure, hornlets, dental cusplets, new dental folds and plications). These characters are also germinal in origin, but, unlike saltations, they develop orthogenetically and very gradually and never appear at first as complete structures. They are invariably normal.

4. *Proportion biocharacters.*—Allometrons of Osborn, quantitative biocharacters, plus and minus proportions, skull proportions (such as dolichocephaly and brachycephaly), limb proportions (such as dolichomely and brachymely, adaptive or neutral). These are all proportional, quantitative, in existing units of structure. Unlike saltations and rectigradations they may first appear in ontogeny, in the body, and subsequently in

the germ. Whatever their cause or origin they become true germinal biocharacters, separable in heredity and developing orthogenetically.

All these four kinds of biocharacters are observed in many complete series of fossils. In the titanotheres the rise of rectigradation and proportion biocharacters constitutes dominant modes of evolution. The saltations seem to be abnormalities or defects in the germ and do not appear to play any part in the modes of evolution of the titanotheres. Theoretically (Darwin) the minor fluctuations of proportion may afford the material out of which certain new adaptive proportional characters are evolving.

The six problems in biocharacter evolution in the body and germ are as follows:

1. Genesis, initiation of new biocharacters: Do they arise suddenly or continuously?
2. New proportions: Do proportions arise suddenly or gradually?
3. Correlation: How are biocharacters correlated?
4. Velocity: How are the motions of biocharacters regulated?
5. Heritage: What is the behavior of mingled biocharacters?
6. Genesis: Do new biocharacters first appear in the body or in the potentiality of the germ?

SEPARABILITY AND COORDINATION OF BIOCHARACTERS

Although in certain principles of form (morphology) and function (physiology) as well as of inheritance (heredity) biocharacters are separable, in other aspects they are closely coordinated and correlated with other biocharacters so as to play their part in the organism. Consequently biocharacters in course of development display a great number of different and invariably correlated modes of evolution. Five principles of the evolution of biocharacters are set forth below.

I. *Origin, genesis*

1. Saltations, major.
2. Saltations, minor; mutations of De Vries.
3. Continuous genesis of rectigradations.
4. Sudden genesis of new proportions.

II. *Proportion, genesis*

1. Fluctuation, plus and minus variation.
2. Continuous evolution of proportion.
3. Influence of habit.
4. Influence of internal secretions.

III. *Cooperation, coordination*

1. Compensation in development and degeneration.
2. Grouping or correlation of function.
3. Mechanical interrelation of separate parts.
4. Linkage of biocharacters with male or female sex, respectively.
5. Coordination by internal secretions.

IV. *Motion, velocity*

1. Acceleration in ontogeny.
2. Retardation in ontogeny.
3. Acceleration in phylogeny.
4. Retardation in phylogeny.
5. Arrest of development in phylogeny.
6. Acceleration or retardation by internal secretions.

V. *Heritage*

1. Biocharacter heritage, separability, segregation.
2. Biocharacter heritage blending, intermingling forms of biocharacters from two separate parents or strains.
3. Biocharacter heritage, "specificity" in strict repetition of parental or racial character.
4. Separability and blending of proportions.

INITIATION OF BIOCHARACTERS: IS IT ENVIRONMENTAL, ONTOGENETIC, OR GERMINAL?

Modes of initiation.—The observed time and place of the visible initiation or genesis of each new biocharacter, whether environmental, somatic, or germinal, is a matter of first importance. There are contrasts—for example, the visible genesis of each cusp rectigradation is at birth; the visible genesis of each horn rectigradation is in the adult. Does this mean that the new cusps and new horns have different causes?

In the observation of each biocharacter it is desirable to make the following notes as to its initiation.

Initiation in origin: Is the first appearance germinal or somatic? For example, all rectigradations in the teeth so far as observed make their first appearance in the germ.

Initiation in motion (acceleration, retardation, balance, arrest): Is it germinal or somatic? For example, does the initiation in velocity make its first appearance in the germ or in the body? In most animals the acceleration of characters in ontogeny and phylogeny is purely germinal, as in the limb proportions of praecoces (birds and quadrupeds that are capable of rapid motion at birth).

Initiation in form evolution (rectigradations, allometrons): Is it germinal or somatic? For example, although all known rectigradations are congenital, many allometrons may arise first in the soma.

Initiation in cooperation, coordination, correlation, compensation, sex linkage, etc.: Is this germinal or somatic? Besides the congenital correlation of form and function many kinds of coordination arise ontogenetically.

Germinal initiation.—Close observation of the time of the initiation of each biocharacter, whether obviously environmental in its first appearance or obviously ontogenetic, is very important. Certain proportion characters, such as the proportions of the skull, apparently arise in the germ; other proportion characters may first appear somatically through the use and disuse of parts, as for example in the limbs. We are absolutely sure that the initiation of many biocharacters is germinal, whatever may be their causes. This is particularly true of the rectigradation cusps of the grinding teeth. Again, the rudiments (recti-

gradations) of new cusps on the grinding teeth are developed in the jaw long before birth; obviously their first appearance is germinal. In apparent but not actual contrast, the rudiments (rectigradations) of horny outgrowths upon the skull first appear in late ontogenetic stages; after a long period of geologic evolution these appear at birth or before birth as germinal biocharacters. This leaves open the question whether the initiation of the horns of the titanothere is somatic or germinal. Followers of Lamarck, Spencer, and Cope would contend that as the horns first appear in late stages of somatic development the initiation is somatic (ontogenetic)—that horns first appear as the results of growth, localized by habit. This question is discussed below under the heading "Horns arise as typical rectigradations."

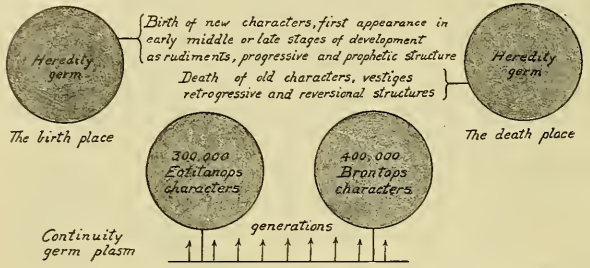


FIGURE 728.—Germinal origin and disappearance of characters

Showing that the germinal cycle of certain biocharacters, such as rectigradations and certain allometrons, first appears in the germ and that after a long period of acceleration and visible evolution in the soma these biocharacters may undergo retrogressive evolution or retardation and may be retained in the germ as latent or potential predispositions and reappear in the soma only occasionally as reversional structures. This kind of germinal velocity, or character movement, is clearly observed in the lateral digits of the horse.

DIFFERING HEREDITARY VELOCITIES; RATES OF MOTION OF BIOCHARACTERS

Definitions.—The term velocity applied to a biocharacter refers to its separate rate of development in the body (ontogeny) as well as to its separate rate of appearance in evolution (phylogeny). These two kinds of hereditary velocity are quite distinct from each other and are both, in different ways, highly adaptive. The resemblances and contrasts between these two kinds of biocharacter velocity are shown in the following principles and examples.

Ontogenetic velocity of biocharacters.—The movement of biocharacters has been demonstrated both in embryology (Agassiz; Haeckel, biogenetic law) and in paleontology (Hyatt, 1866.1, law of acceleration and retardation). The principle as developed by Hyatt and Cope (1887.1, 1896.1) in paleontology is that biocharacters which may originate at or near adult development of the individual may be inherited in successive generations in earlier and earlier stages of individual development until they exist only in the extremely young or are actually skipped as stages of development. In the titanotheres, for example, the horns first appear as rudiments in adult stages of individual development, but after a very long geologic interval they are thrust forward into prenatal stages, so that the young titanotheres have horns at birth. Such characters are said to be accelerated. Other characters are ontogenetically retarded: they lose their ontogenetic velocity. For example, the lateral digits of the horse are so slowed down in rate of development that finally they are confined to the germinal stage, in which we find a vestige of one terminal phalanx (Ewart, 1894.1), which is never present in the young (fig. 730, B_1). This gradual acceleration or retardation of biocharacters furnishes one of the most striking examples of continued evolution in adaptation; one "genus" or "species" slips gradually into another (for example, *Merychippus* into *Pliohippus*) not through the sudden or abrupt falling out of a character but through the adaptation, acceleration, or retardation of certain similarly functional biocharacters.

Phylogenetic velocity of biocharacters.—Phylogenetic velocity is a quite different property of biocharacters from that described above. It is a property discovered and demonstrated by Osborn in the researches made for this monograph, namely, that certain similar biocharacters which are commonly regarded in comparative anatomy as "homologous,"[54] "homogenous," "homorphous," really arise independently, although they appear at earlier stages of geologic time in certain phyla of the titanotheres than in others. For example, all the five or six branches of Eocene titanotheres eventually exhibit horn rudiments, rudiments that evolve gradually into "homologous" horns. These horn rudiments are well developed in the adult stages of certain phyla, whereas in other phyla the skulls are still hornless; in other words, each phylum

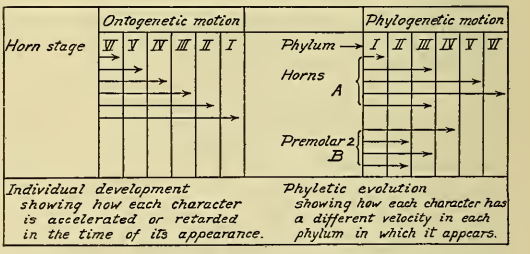


FIGURE 729.—Contrast between the ontogenetic and phylogenetic velocity of a biocharacter

In its ontogenetic velocity the horn rectigradation appears in all titanotheres in a late stage of individual development, which we may call stage VI. Through ontogenetic velocity it is thrust forward until it finally appears in stage I, before birth. In B the same biocharacters (that is, the horn rectigradations and cusp rectigradations) exhibit a different phylogenetic velocity in each one of the six phyla of titanotheres in which they independently arise.

[54] Homology in the strictest sense is homogeny—that is, direct derivation of a character from the germ of a similar antecedent ancestral character.

has its distinctive velocity of the horn biocharacter; and the same is true of the new cusps appearing on the teeth.

Therefore when we compare similar biocharacters of every kind in two distinct phyla of the titanotheres we find that not only the horns but every biocharacter has

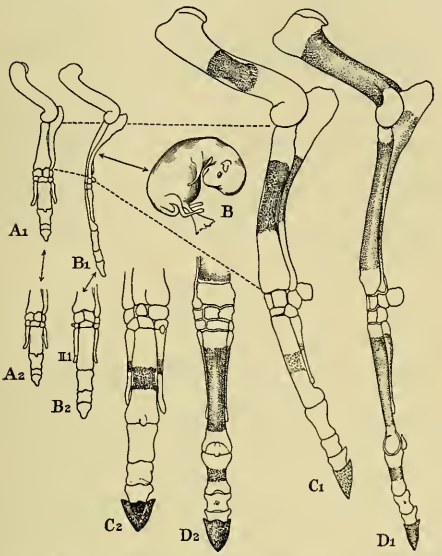


FIGURE 730.—The limbs of four embryos, showing the ontogenetic velocity of the bones of the fore limb in horses

A, 20 millimeters, to D, 350 millimeters. After Ewart, 1894 (Pl. 1D), rearranged. Observe the acceleration of proportions in the forearm and manus.

its distinctive phyletic velocity. For example, close examination by Gregory of the actual percentage increments of proportions in the evolving *Palaeosyops* skull demonstrates three principles of motion, namely, (1) that each cranial, dental, and skeletal biocharacter is evolving at a different rate, some faster, some slower; (2) that a biocharacter which early in geologic time evolves rapidly may afterward evolve more slowly, while the velocity of other continuous proportion biocharacters may be increasing; (3) that the movement of a biocharacter may be reversed, so that after a long period of phyletic velocity it may take an opposite direction.

The following five principles of biocharacter velocity are well established in this monograph:

1. All biocharacters are moving, each having its separate velocity; the movement is either progressive or retrogressive.

2. The phyla of titanotheres are distinguished by relative rates of velocity of similar biocharacters in geologic time, also by the acceleration or retardation of similar biocharacters in ontogeny.

3. This biocharacter velocity may be cumulative and run to an extreme—that is, to overdevelopment of certain organs and structures.

4. Juxtaposed biocharacters may show entirely distinct velocities.

5. The retrogression and subsequent recession of a biocharacter may reverse the order of its appearance.

Having discussed the interpretation of the various phenomena which are observed in the evolution of biocharacters in titanotheres we are ready to interpret the evolution of other series of American quadrupeds, such as horses, rhinoceroses, elephants, which are now under observation by Osborn.

MODES OF BIOCHARACTER EVOLUTION ACTUALLY OBSERVED

MAMMALIAN PHYLA DISTINGUISHED BY DIFFERENT ONTOGENETIC AND PHYLOGENETIC VELOCITIES IN THE SAME BIOCHARACTERS

Members of different phyla may possess exactly the same biocharacters, but each of these biocharacters may exhibit a different rate of phylogenetic progress. It is by these contrasts in the rate of evolution of a large number of similar biocharacters that the phyla of titanotheres and of other mammals may be clearly distinguished. In 1902 the fact was established that throughout the whole geologic period when the *Titanotherium*-bearing beds (Chadron formation) were being deposited as many as eight different phyla of

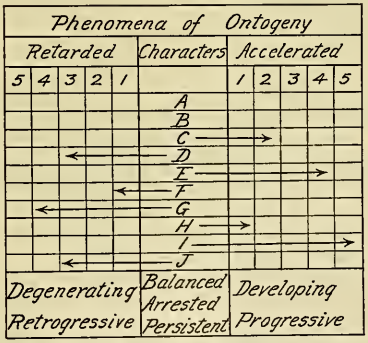


FIGURE 731.—Relative velocities (acceleration, balance, or retardation) of a series of biocharacters (A–J)

Some are progressive, developing rapidly; others, though adjacent, are balanced or are retrogressive and degenerate.

titanotheres were independently evolving in the same general region. These eight phyla correspond more or less closely to the several "genera" originally proposed by Cope and Marsh.

Study of these separate phyla by the author with the cooperation of Dr. W. K. Gregory was directed to show what each of these phyla was like at the beginning of the deposition of the *Titanotherium*-bearing

beds and what each was like at the end, and thus to compare the beginning and the end of each phylum in respect to its several biocharacters. Measurements were made of the elements shown in the accompanying table, including (1) length of skull, (2) breadth of skull, (3) cephalic index, (4) length of superior grinding teeth, (5) length of horns, and each titanothere phylum is seen to have its absolute increase, represented by the plus sign (+). In a sixth part measured, the length of the nasals, there is an absolute decrease, represented by the minus sign (−). It is seen that not only are the absolute increments and decrements different in each phylum but that the relative increments and decrements are distinctive.

Maximum increase or decrease (in males) of certain elements in phyla distinguished by different rates in the genesis and transformation of biocharacters during the deposition of the Titanotherium beds

[All figures approximate]

	Menodontine group (short-horned)				Brontotheriine group (long-horned)	
	Mesaticephalic to brachycephalic		Mesaticephalic to dolichocephalic		Mesaticephalic to brachycephalic	
	Brontops	Diploclonus	Allops	Menodus	Megacerops	Brontotherium
Basilar length of skull:						
Percentage	+31	(?)	+17	+36	(?)	+32
Millimeters	+185	(?)	+110	+222	(?)	+215
Zygomatic breadth of skull:						
Percentage	+39	(?)	+67	+15	(?)	+61
Millimeters	+187	(?)	+230	+73	----------	+270
Primitive and progressive cephalic index (limits)	72–87	85–91	67–76	62–70,[a] 79	(?) to 84	66 to 80–87
Superior grinding teeth (premolar-molar series):						
Percentage	+34	(?)	+30	+75	(?)	+25
Millimeters	+96	(?)	+85	+200	(?)	+75
Free length of horns:[b]						
Percentage	+143	(?)	+240	+300	(?)	+260
Millimeters	+122	(?)	+140	+220	(?)	+283
Free length of nasals:						
Percentage	−11	(?)	−31	+33	(?)	−66
Millimeters	−9	(?)	−33	+43	(?)	−76

[a] Estimated.

[b] Height above narial opening.

DISTINCTION BETWEEN RECTIGRADATION BIOCHARACTERS AND ALLOMETRON BIOCHARACTERS

Apparently two kinds of biocharacters arise in the hard parts of titanotheres and other mammals. The difference is observed in their respective modes of origin and evolution. Theoretically we may attribute them to different complexes of causes.

"Rectigradation"[55] (Osborn, 1907.301, p. 228) is a designation for the earliest discernible stage of an absolutely new adaptive character of an orthogenetic kind. Such rudiments of new characters were first termed (Osborn, 1891.53) "definite variations" to distinguish them from the theoretic "indefinite" or "chance" variations of Darwin. When the shadowy rudiment of a new dental cusp or of a new horn first appears it is termed a rectigradation. It marks a numerical change, the addition of the rudiment of a new biocharacter that was not previously present, which when observed in successive generations is found to develop into an important adaptive character.

Quite distinct is an "allometron"[56] (Osborn, 1912.372, p. 250). It is not a numerically new character but a new proportion[57] in an old character, which may be expressed in differences of measurement, in ratios and indices. This evolution of new proportions in existing characters is a quantitative change; although a highly adaptive and important process it adds no new unit to the organism. These changes of proportion in the titanotheres were investigated very carefully by Osborn and Gregory between 1902 and 1916. In the skull there arise such contrasting proportions as brachycephaly and dolichocephaly; in the feet, brachypody and dolichopody. We learn from breeding that both kinds of change, rectigradations and allometrons, are germinal or become so; both become separable in heredity.

As certain differences of opinion and interpretation as to the distinctness of rectigradations and allometrons have arisen between three observers (H. F. Osborn, W. D. Matthew, W. K. Gregory) it is important to state very clearly some of the resemblances and differences between these two kinds of biocharacters.

[55] Rectigradation > *rectus*, straight; *gradus*, step.

[56] Allometron > ἄλλοῖος, different, changed; *μέτρον*, the contents or thing measured; hence alloiometron or allometron, a changed quantity or measurement.

[57] Proportion > *pro*, for; *portio*, share, part; the relation of one thing to another in respect to size, quantity, magnitude of corresponding parts, capacity, or degree.

RESEMBLANCES BETWEEN RECTIGRADATIONS AND ALLOMETRONS AS BIOCHARACTERS

Rectigradations and allometrons have certain points of resemblance: (1) Both are orthogenetic, continuous, or gradual in origin, rather thau discontinuous, saltatory, or tychogenetic (*τύχη*, chance, fortuity; *γένεσις*, genesis); (2) both appear in increasing intensity in successive "ascending mutations" of the same phyla, a new dental cusp, for example, becoming more distinct, the brachycephaly becoming more pronounced; (3) both are subject to similar laws of cellular growth, the rectigradations more localized, the allometrons more diffused; (4) both display differences in phylogenetic velocity; similar rectigradations and allometrons arise in different geologic stages; (5) both display differences in ontogenetic velocity; horn rudiments and skull proportions, for example, may be accelerated or retarded in development; (6) both are subject to the law of correlation, compensation, and coordination with other parts; (7) both may or may not be correlated with sex; (8) after rectigradations such as rudiments of horns have first appeared, they are subject to changes of proportion—that is, to allometrons.

CONTRASTS BETWEEN RECTIGRADATIONS AND ALLOMETRONS AS BIOCHARACTERS

The contrasts between the features of rectigradations and allometrons are shown in the accompanying table.

Contrasts between rectigradations and allometrons

Features of rectigradations	Features of allometrons
1. Rectigradations are strictly new biocharacters—local outgrowths—such as dental cuspules or horn rudiments.	1. Allometrons are generally changes of old proportions not localized—for example, dolichocephaly, brachycephaly, hypsodonty.
2. Rectigradations give rise to so-called "homologies," more strictly "homomorphs"; the mesostyle of *Mesohippus* and that of *Palaeosyops* are said to be homologous, although one animal is not descended from the other, but both are descended from a very remote common ancestor that had no mesostyle.	2. Allometrons give rise to analogies, never to homologies in any sense; dolichocephaly, for example, is an analogous change of the cranium in *Homo* and in *Menodus*.
3. Rectigradations are neomorphs, new outgrowths, numerically new biocharacters—for example, a tooth having three cusps develops five or six cusps.	3. Allometrons are allomorphs, or heteromorphs, or changes of proportion—they are quantitative; a narrow tooth, for example, becomes a broad tooth.
4. Rectigradations appear chiefly in near or remote descendants of common ancestors; the mammals of the order Perissodactyla, for example, evolve many similar rectigradations in their grinding teeth which do not appear in the teeth of the Artiodactyla or the Amblypoda.	4. Allometrons are totally independent of remote ancestral affinity—for example, Perissodactyla, Artiodactyla, Amblypoda may alike become dolichocephalic. They are partly independent of near ancestral affinity; nearly related races of men of the same species (*Homo sapiens*) become dolichocephalic or brachycephalic.
5. Rectigradations apparently have little or no observable adaptive value at their origin, little or no selection survival value.	5. Allometrons may have adaptive or mechanical significance throughout; they may consist of changes of limb proportion, which appear to be adaptable or inadaptable throughout their evolution.
6. The origin of similar rectigradations in independent phyla of mammals and families of mammals always gives rise to parallelism, convergence—for example, the molar teeth of *Eohippus*, a horse, converge toward those of *Notharctus*, a lemur, in the independent origin of similar cuspules.	6. The origin of allometrons in animals of the same ancestry or of nearly allied strain may give rise either to convergence or to divergence; a dolichocephalic phylum, for example, may diverge from a brachycephalic phylum.
7. Rectigradations are not known to be produced experimentally in ontogeny. So far as observed they are from the beginning germinal biocharacters.	7. Allometrons may be produced experimentally in ontogeny; new limb proportions, for example, may arise from new or modified habits. All allometrons are not certainly known to be germinal at the beginning.
8. Rectigradations as neomorphs are relatively rare or infrequent in mammals; see Miller's definitions of the species of European mammals (1912.1).	8. Allometrons are universal phenomena, constantly appearing in specific definition; see Miller, op. cit.
9. Rectigradations may be measured by indices and ratios only after they have developed to a sufficient size—for example, changes of proportion in horns and cusps (allometrons).	9. Allometrons constantly afford changing indices and ratios in all stages of ontogeny and of phylogeny.
10. Rectigradations characteristic of a phylum in one geologic period may appear in rudimentary form at a later period in another phylum as "homomorphs"—such as the enamel folds known as crista, crochet, antecrochet in horses, titanotheres, rhinoceroses.	10. Similar or dissimilar allometrons may arise in related phyla at different periods of geologic time.

Contrasts between rectigradations and allometrons—Continued

Features of rectigradations	Features of allometrons
11. Rectigradations appear to indicate a germinal predisposition or predetermination to vary in the same direction, these predispositions being most apparent in the more closely related phyla and less apparent in remotely related phyla.	11. Similar or entirely dissimilar allometrons may arise in closely related branches of the same stock; dolichocephaly and brachycephaly, for example, may arise in closely affiliated branches of *Homo sapiens*.
12. The rise of similar rectigradations may confidently be predicted in geologic descendants of similar phyla—for example, similar and convergent rectigradations successively develop in the premolar teeth of the entire order Perissodactyla.	12. Occurrence of similar allometrons can never be predicted; even within the family Brontotheriidae, even within the genus *Telmatherium*, dissimilar and divergent allometrons may arise during the same geologic stage.

Theoretic conclusions concerning predisposition to vary (Osborn)

Causes of rectigradations	Causes of allometrons
13. Rectigradations appear to be due in part to germinal potentialities as to definite or determinate variation which are found in the common ancestors of several phyla. The apparent potentiality to definite variation may be analogous to the similar mutations (De Vries) arising from the same stocks. (See section on causes of evolution, p. 834.)	13. Allometrons exhibit hereditary predispositions and definite variations only within descendants of the same phylum—for example, a certain brachycephalic or dolichocephalic tendency once displayed within a phylum seems to be cumulative in successive generations.
14. Similar rectigradations arise in connection with changes of environment and of habit (or ontogeny), but it is not known whether there is any real causal relation between changes of environment and of ontogeny and the origin of definite rectigradations like dental cusps and horns.	14. Allometrons are also directly observable as the result of changes of environment and of habit, but it is not known whether these are merely somatic, ontogenetic, or are actually germinal.

PRINCIPLES OF RECTIGRADATION

HORNS ARISE AS TYPICAL RECTIGRADATIONS—ORTHOGENETIC, CONTINUOUS

Phylogenesis of horns in the titanotheres.—Horns are biocharacters having very complex germinal and somatic relations. That they are separable in heredity is shown by the sudden and complete disappearance of horns in certain domestic breeds of cattle and by the sudden appearance of rudiments of horns as major saltations in many orders of mammals that are naturally hornless. Horns are typical rectigradations in the titanotheres, as distinguished from allometrons, for the following seven reasons:

1. Horns arise from excessively rudimentary beginnings—inconspicuous bony swellings which in their initial stages can hardly be detected on the surface of the skull.

2. These horn rudiments arise independently in the same region of the skull in different phyla of the titanotheres at earlier or later geologic periods, respectively.

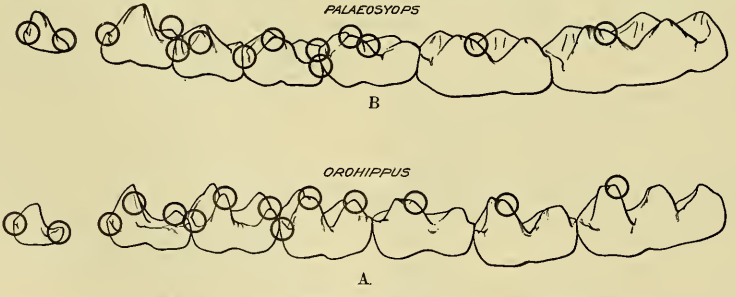


FIGURE 732.—Rectigradations in the teeth of Eocene ungulates

A, *Orohippus* sp., a primitive equine; B, *Palaeosyops paludosus*, a primitive titanothere. From specimens in the American Museum of Natural History. Internal view of the lower teeth. The circles mark the cusps, which appear independently in the phyla of the horse and the titanothere. They are at first barely visible but increase in size in successive geologic levels.

3. The horn rudiments evolve continuously and very gradually change in form and proportion (allometrons).

4. In the earliest geologic stages in which horns have been observed they are found only in adult individuals, but through ontogenetic acceleration

they are gradually pushed forward into younger and younger ontogenetic stages until finally they appear on the skull before birth.

5. The horn rudiments, through phylogenetic acceleration or retardation, appear at earlier or later geologic stages in certain phyla than in other phyla (fig. 734).

shape of the horn (fig. 733) is like that seen in the ontogeny of the horns of cattle.

Ontogenesis of the horns of cattle.—The ontogenesis (development) of the bony horns of domestic cattle (Pl. XLV) appears to be closely similar to the phylogenesis (evolution) of the horn rectigradations in titanotheres. The comparison is useful. The horn biochar-

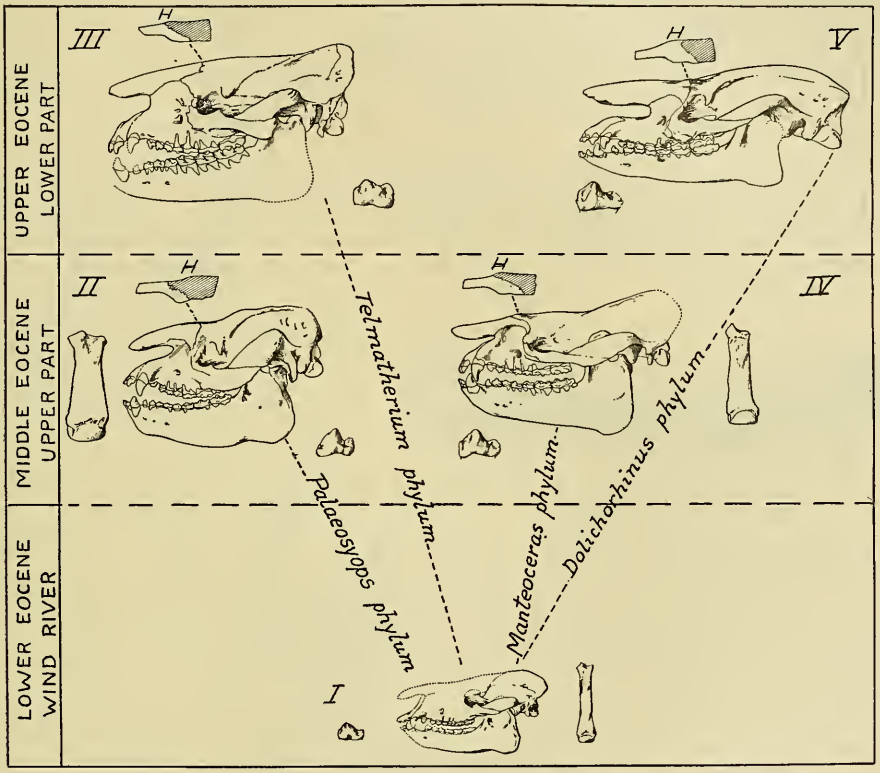


FIGURE 733.—Rectigradations and allometrons in the skulls, teeth, and feet of titanotheres

Rectigradations are shown on the cuspules of the lower second premolar teeth; allometrons are shown in the proportions of the head (brachycephalic, mesaticephalic, dolichocephalic); allometrons are shown in the proportions of the median metacarpal (dolichopodal, mesatipodal, brachypodal). I, *Eotitanops*, an ancestral lower Eocene mesaticephalic, dolichopodal titanothere; II, *Palaeosyops*, a broad-headed (brachycephalic), broad-footed (brachypodal) upper middle Eocene titanothere; III, *Telmatherium*, a medium-headed (mesaticephalic) upper Eocene titanothere; IV, *Manteoceras*, a medium-headed (mesaticephalic), medium-footed (mesatipodal) middle Eocene titanothere; V, *Dolichorhinus*, a long-headed (dolichocephalic) short-footed (brachypodal) upper Eocene titanothere. II–V represent four independent phyla of Eocene titanotheres which are widely divergent in the allometric evolution of the head and of the feet but are convergent in the independent evolution of similar cusp rectigradations on the teeth and similar horn rudiments (H) on the skull.

6. At the time of their first appearance horns seem to be equally developed in both sexes, but gradually they become much larger and more formidable in the males than in the females.

7. In the titanotheres the horn swelling rises at the junction of the nasals and the frontals (black shading in fig. 733). It is borne chiefly on the nasals in dolichocephalic skulls, chiefly on the frontals in brachycephalic skulls. The original low, rounded

acter in cattle is known to involve a large number of coordinated and correlated biocharacters, all of which are germinal in origin, namely: (1) A psychic predisposition to use the horn, which is manifested at or soon after birth; (2) a thickening of the epidermal cells above the bony horn rudiment, which in ontogeny appears earlier than the bony rudiment itself; (3) early agglutination of the hair to form the rudiments of the horny sheath; (4) appearance of the bony swelling,

the osseous horn, at the junction of the frontals and parietals (Pl. XLV, C); (5) shifting of the frontals and the osseous horns to the back of the cranium through allometry; (6) internal secretions from the interstitial cells of the male (testis) or female (ovary) germ glands.

the junction of the frontals and parietals, the shifting of the osseous horns forward from above the eyes, and the changes in size and proportions, described in Chapter V, section 2, and Chapter X, section 3.

The horn rudiments in different phyla, like the cusp rectigradations, show marked differences in phylo-

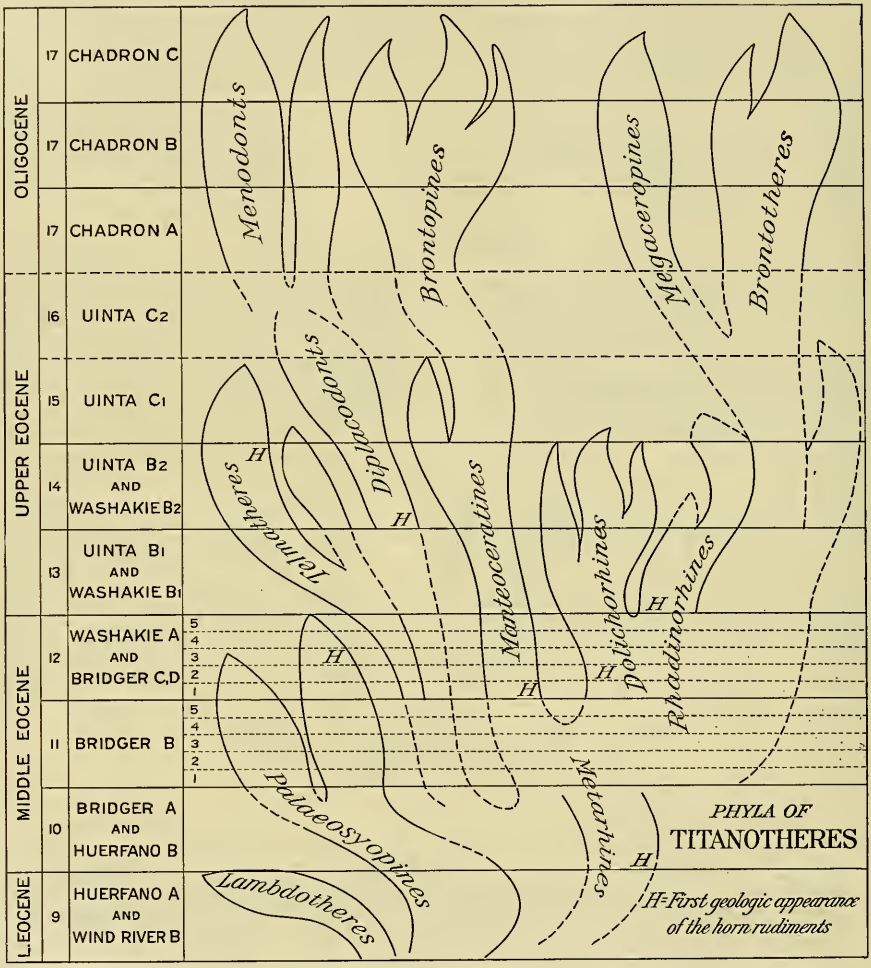


FIGURE 734.—Independent appearance of rudiments of the horn (*H*) at different stages of geologic time, though in the same part of the skull, in different phyla of the titanotheres

PHYLOGENESIS AND INITIATION OF HORNS IN TITANOTHERES [58]

In contrast to the development of the horns of cattle all that we paleontologists observe in the evolution of the horns of the titanotheres is the rudimentary appearance of the bony swelling of the osseous horns at genetic and ontogenetic velocity. One of the most significant discoveries made concerning the titanotheres is that their horn rudiments arise long after the phyla have been separated from one another, earlier in some phyla and later in others, but always on substantially the same part of the skull. This is probably true in general of the origin of horns in mammalian families. Each family probably has its predisposition to develop

[58] See detailed descriptions in Chapter V.

horns in a certain way, but in each this predisposition manifests itself at different times. According to the Lamarckian principle, the germinal psychic predisposition to use the horn should appear first, and this initiation should be followed after a certain period by the ontogenetic bony horn rudiment due to habit, but there is no evidence for this sequence. The horn rectigradations, like the cusp rectigradations, seem to be initiated as a germinal phenomenon; it would appear that the psychic tendency and the horn rudiment appear simultaneously, but as yet there is no positive evidence on this important matter of initiation.

DENTAL RECTIGRADATIONS

The grinding teeth of the titanotheres are sluggish in evolution as compared with those in other perissodactyls, especially the horses, in which the grinding teeth are rapidly accelerated in evolution. Nevertheless they exemplify even more perfectly than the horns the modes of rectigradation. Interest in the cusp evolution is enhanced by the fact that the cusp rectigradations in the lower teeth are mechanically coordinated and timed with the cusp rectigradations in the upper teeth. The causes of this constant and perfect mechanical adjustment of the rectigradations and allometry of the upper and lower grinding teeth of titanotheres and other mammals presents one of the most difficult problems in germinal evolution, the various explanations of which will be discussed in the third part of this section, under the heading "Theoretic causes of evolution." Here it may be sufficient to point out the modes of rectigradation without making reference to the theory of the underlying causes.

The adaptive cenotelic (Gregory, 1910.1, 1914.1) principle in the rectigradations and allometrons of the titanotheres, as in all other perissodactyl quadrupeds, is to molarize the premolar teeth—that is, to convert the premolars into teeth of the molar pattern, adaptively because a herbivorous animal can more effectually crush and grind its food with six complete grinders (molars and molariform premolars) than with three complete grinders (molars) and three incomplete grinders (premolars). As shown in detail in Chapter V this molarization takes the same course in all the Eocene titanotheres, namely:

1. Molarization generally, but not invariably, is first introduced in the fourth premolar ($p\frac{4}{4}$), which is usually the most progressive tooth of the premolar series. Thus, these teeth are the first to acquire a partial molar pattern. (For an exception, note *Palaeosyops copei*.)

2. The molarization in $p\frac{4}{4}$ and the other premolar teeth of the titanotheres never attains the same degree of mechanical perfection that it does in the horses; the premolar teeth never become exactly like the molars—they are not perfectly molarized.

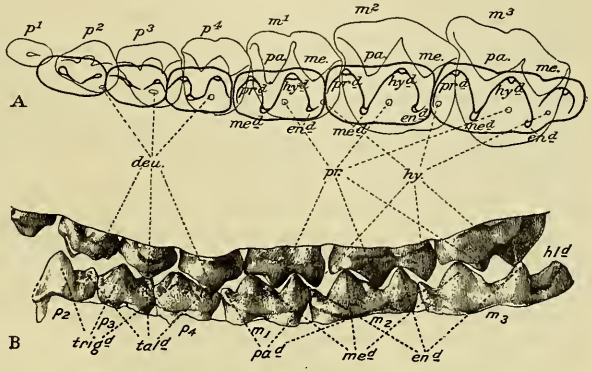


FIGURE 735.—Cusp rectigradations in *Telmatherium*

The cusp rectigradations in the lower teeth are coordinated and timed with the cusp rectigradations in the upper teeth, as shown here in the occlusion of the jaws of *Telmatherium cultridens*, Princeton Mus. 10027 (type); one-half natural size. After W. K. Gregory. A, Crown view, lower teeth (heavy lines) superposed on the upper teeth (light lines); B, inner side view.

3. The molarization advances at a uniform rate, respectively and successively, in $p\frac{4}{4}$, $p\frac{3}{3}$, $p\frac{2}{2}$, in the order named, but affects only slightly $p\frac{1}{1}$. This phylogenetic acceleration of the premolar rectigradations is more rapid in $p\frac{4}{4}$ and less rapid in $p\frac{2}{2}$.

4. It follows that the fourth upper and lower premolars ($p\frac{4}{4}$) pass through a series of stages of rectigradation, which are taken up successively and passed through by $p\frac{3}{3}$, $p\frac{2}{2}$, whereas $p\frac{1}{1}$, with its simple mechanical crown, retains its remote ancestral condition.

These four stages of molarization are illustrated in Figures 732, 735, and the accompanying analytical table

Mechanically correlated rectigradations and allometrons of the upper and lower premolar teeth of titanotheres (Palaeosyops)

Lower premolars	Upper premolars
1. The conical tooth or protoconid p_1 becomes elongate anteroposteriorly; rudimentary anterior and posterior ridges run down from summit to base, becoming more sharply marked and deflected linguad at the base; concomitantly the single fang tends to become divided. Total, one cusp.	1. The laterally compressed conical tooth p^1 exhibits ridges on the anterior and posterior faces and a continuous internal cingulum; the crown is a protocone. Total, one cusp.
2. In p_2 the posterior vertical cingulum ridge acquires a deep notch about halfway up the crown of the protoconid, separating off a posterior lobe (or hypolophid); the tooth broadens transversely, and the anterior and posterior fangs become wholly separate; a rudimentary paraconid is seen. Total, three cusps.	2. The triangular second premolar p^2 consists of the high protocone; externally devoid of cingulum, internally the cingulum gives rise to the well-developed deuterocone; while on the posterior ridge of the protocone is a very slight swelling which indicates the rudiment of the tritocone. Total, three cusps.
3. In p_3 the paraconid becomes stronger; the hypolophid or posterior lobe grows higher; the protoconid broadens at the top, producing finally a well-marked oblique crest (or metalophid); concomitantly the hypoconid lobe becomes broader than the protoconid lobe; concavities appear on the internal face of both cusps; by the deepening of these concavities the anterior and posterior crests or metalophid and hypolophid become sharply defined. Total, three cusps, a rudimentary protolophid, a metalophid, and a hypolophid.	3. The third premolar p^3 now has a true ectoloph, with the rudiment of a parastyle, and an incomplete external cingulum; the deuterocone is larger; it is embraced on the posterior as well as the anterior side (but not lingually) by the cingulum; it exhibits a faint anterior crest or protoloph; the tritocone nearly equals the protocone in size. Total, four cusps, an ectoloph, and a rudimentary protoloph.
4. In p_4 the paraconid is slightly stronger; the transverse ridge at the summit of the protoconid divides, by the insinking of an anteroposterior nick, into the protoconid proper and the metaconid, thus completing the protolophid; the posterior face of the hypoconid broadens into the hypolophid; the valley separating the protolophid from the hypolophid becomes straighter and more transverse, and thus these anterior and posterior crests become more symmetrical. Total, four cusps and two crests.	4. The fourth premolar p^4 exhibits a still more pronounced external cingulum, a prominent parastyle, a subequal protocone and tritocone, between which is the faintest rudiment of a mesostyle. The deuterocone is still larger and not yet surrounded basally by the cingulum; it exhibits a slightly stronger anterior crest or protoloph, on which is seen a small protoconule. Total, six cusps, an ectoloph, and a protoloph.
The molarization of p_4 is now complete except that an entoconid is not developed until the tetartocone is developed above.	The molarization of p^4 is now complete except that a tetartocone is not formed until the entoconid is formed below (as in *Diplacodon*).

Summarizing this numerical addition of rectigradation cusps we get the following results in the comparison of similar teeth from successive levels.

Number of rectigradation cusps on lower premolars of Eocene titanotheres

	Wind River	Lower Bridger	Upper Bridger
First premolar	1	1	1
Second premolar	2	3	3
Third premolar	3	3	4
Fourth premolar	4	4	5
	10	11	13

As stated above, this successive numerical addition of cusps as rectigradations affords one means of arbitrarily dividing the stages of evolution in each of the phyla and of naming them species, in the Linnaean sense, and mutations, in the Waagen sense, in a manner similar to that commonly employed for other quadrupeds.

RECTIGRADATIONS OF OSBORN CONTRASTED WITH MUTATIONS OF WAAGEN

Osborn's rectigradations, which are single characters, differ from Waagen's mutations, which are subunits of classification or taxonomy. One or more of Osborn's rectigradations when followed through a series of stages would constitute the subspecific stage known as a "mutation of Waagen." The same rectigradations (homomorphs) appear on the premolar teeth of one or more independently evolving phyla, but in the rectigradation cusps, as in the rectigradation horns, each phylum exhibits its own rate of evolution for each rectigradation, as well as its own phylogenetic velocity or rate of change.

The following table presents crudely the actual modes of evolution in monophyletic, diphyletic, and triphyletic series of titanotheres, terminating in three "genera," A, B, C.

Rectigradations in monophyletic, diphyletic, and triphyletic series, including genera, species, and ascending mutations of Waagen

Geologic level of the Bridger	Three-branch or triphyletic series (genus A)			Two-branch or diphyletic series (genus B)		Single-branch or monophyletic series (genus C):
	Mutations of species A^1	Mutations of species A^2	Mutations of species A^3	Mutations of species B^1	Mutations of species B^2	Mutations of species C
Horizon C 1e (top)	A^{1e}	----------	A^{3d}	B^{1e}	B^{2d}	C^{1e}
Horizon B 2e	A^{1d}	----------	A^{3d}	B^{1d}	B^{2c}	C^{1d}
Horizon B 1, 1	A^{1c}	A^{2b}	A^{3c}	B^{1c}	B^{2b}	C^{1c}
Horizon A 3	A^{1b}	A^{2a}	A^{3b}	B^{1b}	B^{2a}	C^{1b}
Horizon A 2, 2	A^{1a}	a^2	A^{3a}	B^{1a}	b^2	C^{1a}
Horizon A 1, 1 (bottom)	A^1	A^2	A^3	B^1	B^2	C^1

The table begins with three "Linnaean genera," A, B, C, each genus corresponding to one to three phyla, and each genus persisting throughout a long geologic period, namely, from horizon A 1, 1 to horizon C 1e. The table represents thirty-four "ascending mutations" of Waagen, distinguished by the successive addition of new rectigradations (1, 2, 3, etc.) and by changes of proportion (allometrons) (a, b, c, d, etc.).

Tracing each phylum from the lowest to the highest geologic level through ascending mutations we observe that

Mutation A^{1e} may exhibit four new rectigradation cusps and final allometrons.

Mutation A^{1d} may exhibit three new rectigradation cusps and subfinal allometrons.

Mutation A^{1c} may exhibit two new rectigradation cusps and intermediate allometrons.

Mutation A^{1b} may exhibit one new rectigradation cusp and incipient allometrons.

Mutation A^{1a} may exhibit no rectigradations and no changes of proportion.

"MUTATIONS" AND "SPECIES"

Reading horizontally on any given geologic level, say horizon A, level 2, 2, we may discover six "ascending mutations" of Waagen, namely, A^{1a}, a^2, A^{3a}, B^{1a}, b^2, C^{1a}, as shown in the table above.

This entire geologic section of the Eocene theoretically shows, among the 34 ascending mutations of Waagen, 6 Linnaean species: $A^{1\text{-}1e}$, $A^{2\text{-}2b}$, $A^{3\text{-}3d}$, $B^{1\text{-}1e}$, $B^{2\text{-}2d}$, $C^{1\text{-}1e}$.

Thus, through the contemporaneous evolution at different phylogenetic velocities of "homologous" (more strictly "homomorphous") rectigradations and allometrons new rectigradations and proportions at their first appearance correspond with the least or minimal systematic divisions of the zoologic systematist. When a number of these biocharacters continue to progress they constitute the "ascending mutations" of Waagen; when a number of these ascending mutations are similarly grouped they become the "species" of Linnaeus. Therefore the simultaneous evolution of a large number of biocharacters at different rates of evolution constitutes the divergence of character that underlies both the old zoologic and the new paleontologic classification.

These terms and distinctions, which are very difficult to express or to understand in descriptive text, are readily comprehended when members of five or six independently evolving phyla are compared in the museum, character by character, or as shown in the plates and synthetic diagrams.

This mode of dental evolution through rectigradation and allometry is precisely what we observe in other families of mammals, such as the Equidae, the Rhinocerotidae, the Canidae.

HERITAGE SEPARABILITY OF RECTIGRADATION DENTAL CUSPS AND FOLDS

The different rates of development of the premolar cusps indicate that they are true biocharacters, because they display germinal (that is heritage) separability. Exactly similar homomorphous biocharacters appear in the grinding teeth of the horse and of the ass, accompanied by a number of secondary rectigradation enamel foldings and plications. In the hybrid mule, offspring of the male ass and female horse, it is found that these rectigradation folds are completely separated as shown in Figure 736.

RECTIGRADATION CUSPS ON TITANOTHERE TEETH ARE UNLIKE SALTATIONS

In all the hundreds of stages of titanothere dental evolution studied not a single instance has been observed in which a rectigradation cusp and fold appear suddenly, wholly formed; in every instance

the origin of these new cuspules is so contionuus and gradual that they become discernible only after the passage of long periods of geologic time. They are also invariably orthogenetic, evolving in a uniform direction. This mode of evolution recalls the observation of Waagen as to the mode of origin of his mutations. In any large series of titanothere or other mammalian teeth one occasionally finds also major and minor saltations, smaller or larger cuspules, which are usually duplications of the rectigradation cusps, or reversions of former rectigradation cusps, such as the hypocone on the last superior molar.

RECTIGRADATIONS INFLUENCED BY DEGREE OF ZOOLOGIC AFFINITY

The addition of new dental cusps on the teeth and of horn swellings on the skull as rectigradations is influenced by nearness or remoteness of ancestral zoologic affinity. (See predeterminate rectigradation under "Theoretic causes of evolution," p. 834.) Degrees of resemblance in the origin of these new biocharacters always increase with closeness and intensity of kinship. Thus the kinds of rectigradations (whether cuspules or hornlets), as well as the rates of change (phylogenetic velocities), are strongest in phyletic members of the same species; they are somewhat less strong in phyletic members of the same genera; they become increasingly dissimilar as we compare phyletic members of the same subfamilies, orders, etc. Nevertheless the most striking principle in the mode of origin of rectigradations is that similar rectigradations sooner or later tend to appear in descendants of common ancestral forms. This is in striking contrast to the mode of evolution of allometrons; for both dissimilar and similar proportions tend to appear in the descendants of common ancestors.

PRINCIPLES OF PROPORTION

PROPORTION BIOCHARACTERS (ALLOMETRONS)

Changes in proportion common.—Allometrons play a larger part in the evolution of the titanotheres than rectigradations. All the bones of the skull and the skeleton are continuously undergoing a change of proportion—in other words, developing allometrons. Continuous change of proportion is a dominant mode of titanothere evolution; the addition of new parts and the loss of old parts have been second in importance. It is demonstrated throughout this monograph and summarized in the comparative measurements and various tables that all changes of proportion, as a whole, represent the sum of changes of separable parts, biocharacters, each of which has its own rate of evolution. For example, if the top parts of a titanothere skull (*Dolichorhinus*, see below) evolve more rapidly than the bottom parts, the axis of the skull must be bent downward, and the skull as a whole in consequence becomes cyptocephalic; if all the component bones broaden more rapidly than they lengthen the skull becomes brachycephalic.

The causes of changes in the proportions of the skull are probably the same in all other mammals as in man. The processes and results are distinguished as follows:

Process	Result
Uniform lengthening or shortening of all parts—that is, at uniform velocities.	Harmonic facial and cranial structure.
Differential lengthening, shortening, or broadening of certain parts—that is, at different velocities.	Disharmonic facial and cranial structure.

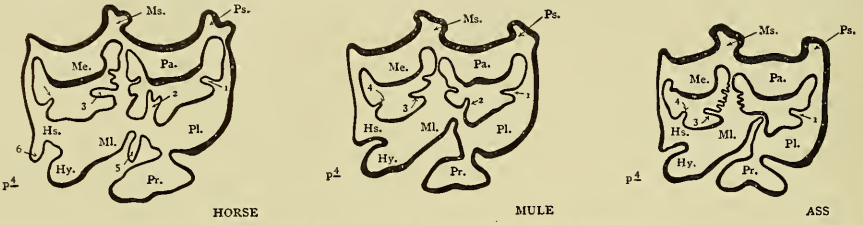


FIGURE 736.—Separability of rectigradation biocharacters in the grinding teeth of the hybrid offspring of a male ass (*Equus asinus*) and female horse (*E. caballus*)

Section through the crown of the fourth superior premolar tooth (p^4) showing that the mule inherits most of the enamel fold rectigradations of the ass but few of those of the horse. After Osborn, 1912.3. The following is a summary of the rectigradation biocharacters in the grinding tooth of the mule:

Distinctly asslike	5	11 peculiar to ass.
Less distinctly asslike	6	
Common to horse and ass	5=5	common to both.
Distinctly horselike	2	6 peculiar to horse.
Less distinctly horselike	4	

Allometrons differential (disharmonic) in origin.—At first glance it would seem that if the bones of the skull were stretched longitudinally as a whole the stretching would give rise to dolichocephaly, or if they were stretched transversely as a whole the stretching would give rise to brachycephaly, and approximately this mode of evolution is seen in skulls where all parts are harmonically lengthened or broadened in nearly equal percentages; but the actual mode of evolution in the titanotheres involves disharmonic and differential lengthening or broadening of each part. On analyzing closely by comparative measurements the progressive changes in titanothere skulls we find that each of the adjacent bony elements acts differently and more or less independently; the skull is not broadened or lengthened as a whole, as if composed of and stretched like India rubber, but each part of it acts as a distinct biocharacter and has its separate velocity or rate of change. This differential principle is illustrated on the accompanying diagram (fig. 738) showing some of the contrasts in the parts evolving in typical broad-headed (*Palaeosyops*) and long-headed (*Dolichorhinus*) skulls.

Allometrons continuous in origin.—Do changes of proportion arise by saltation or continuously? Observations made by the author on titanotheres, rhinoceroses, and horses compared with those made by numerous anthropologists on man demonstrate beyond doubt that all adaptive changes in proportion are continuous in origin; also that, like rectigradations, they take certain directions (from causes which will be considered in the next section) and are cumulative or progressive in successive generations. This kind of proportional change, as demonstrated below, may be suspended or even reversed in direction. This continuity in the evolution of proportions is demonstrated whenever a series that is nearly complete, or unbroken, is measured, as they are in the measurement tables of *Menodus*, *Brontotherium*, and *Megacerops* in the sections treating of these genera. (See Chap. VI.)

Exactly similar results have been obtained by Osborn in the comparative measurement of closely successive series of Oligocene horses. The same is indicated among the Oligocene rhinoceroses but is not yet positively demonstrated. According to the unanimous testimony of anthropologists (Ripley, Races of Europe, 1899.1, p. 624), the form of the human head is the result of very gradual change, either by elongation (toward dolichocephaly) or by broadening (toward brachycephaly). In the native Indian races of America also, which are believed to be of the same remote racial origin, considerable diversity in the proportions of the head has gradually evolved under geographic isolation. Similarly Keith (1911.1) observes that in course of their evolution the tendency of one Negro tribe has been toward the accentuation of one set of skeletal proportions, of another tribe toward another set. The Dinka acquire high stature and narrow heads, the typical Nigerians low stature and narrow heads, the Basoko wide, short heads and low stature, the Buruns broad heads and high stature.

Causes of head allometrons unknown.—It is probable, but not yet demonstrated, that whatever the causes

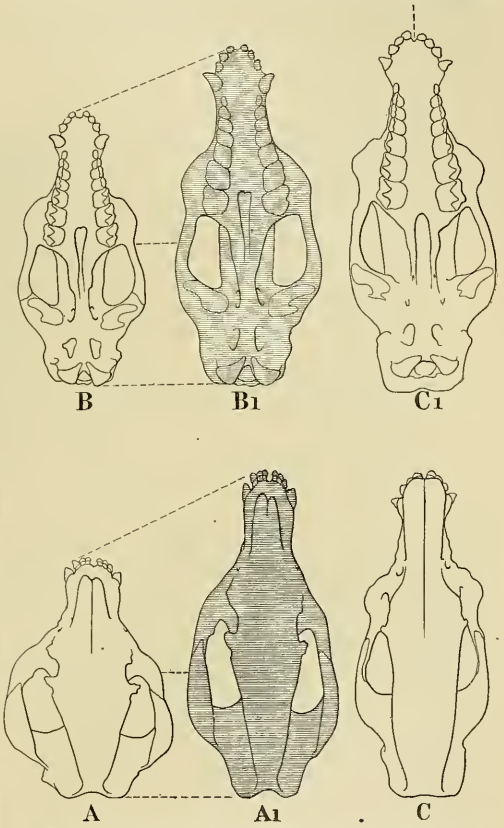


FIGURE 737.—Harmonic and disharmonic natural brachycephaly and dolichocephaly and artificial broadening or lengthening of the outline of a skull

A, *Palaeosyops robustus*, a natural brachycephalic skull; A_1, outlines of the same skull artificially stretched into dolichocephalic form (harmonic); B, *Mesatirhinus megarhinus*, a natural mesaticephalic skull; B_1, outlines of the same skull artificially stretched on India rubber into dolichocephalic form (harmonic); C, *Dolichorhinus hyognathus*, a natural dolichocephalic skull, viewed from above; C_1, *Dolichorhinus hyognathus*, a natural dolichocephalic skull (disharmonic). The contrast between A_1 artificial) and C (natural) and between B_1 (artificial) and C_1 (natural) is clearly displayed.

of proportional change may be they are similar in the evolution of "broad heads," "long heads," "long limbs," "short limbs," etc., among the titanotheres, the horses, man, and all other mammals. In man also there is considerable evidence that the evolution of proportion biocharacters is differential, namely, that while there is often harmonic evolution of head

form, in which all parts are more or less uniformly elongated or broadened together, there may also be disharmonic (that is, differential) evolution of head form, in which certain bony parts, such as the cranium, are lengthened while others, such as the cheek bones, are broadened.

The continuous proportional evolution of the skull of the titanotheres has been demonstrated by the long investigations of the writer and his assistant, Dr. W. K. Gregory, which involved thousands of parative anatomy and in the investigations made for the present monograph.[59] It is as follows:

1. Elongation of the skull as a whole = dolichocephaly.
   Elongation of the cranium only = dolichocrany.
2. Broadening of the skull as a whole = brachycephaly.
   Broadening of the cranium only = brachycrany.
3. Elongation of the face only (that is, proopic dolichocephaly, as in *Equus*) = dolichopy.
4. Abbreviation of the face only = brachyopy.
5. Elevation of the skull and head as a whole, as in *Delphinus* = acrocephaly, hypoicephaly.

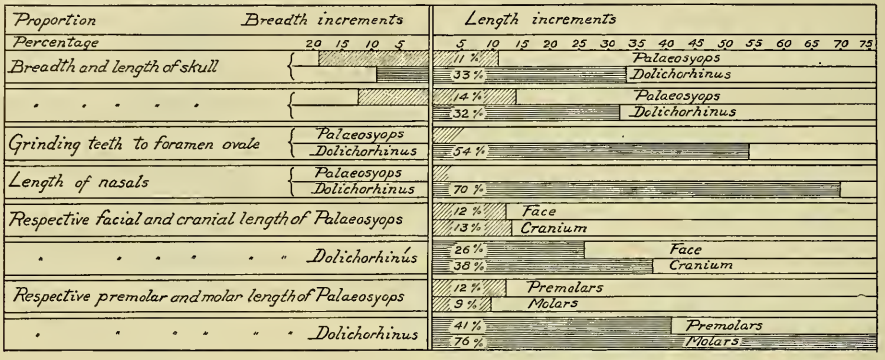


FIGURE 738.—Differential and distinctive increment in every proportional biocharacter group in eight biocharacters of *Palaeosyops* and *Dolichorhinus*

measurements of specimens belonging to a number of successive phyletic series, especially in *Palaeosyops*, *Megacerops*, *Menodus*, and *Brontotherium*. This continuity has been shown in the molar-cephalic index, which is the breadth across the cheek arches × 100 ÷ the basilar length of the skull; also in other indices, such as the faciocranial, in which the continuous trend of proportional change has been carefully measured. It has been demonstrated that elongation of the skull as a whole (dolichocephaly) and broadening of the skull (brachycephaly) may arise independently in every phylum or line of descent.

As shown in Figure 739, the titanotheres, like man, exhibit facial abbreviation (brachyopy) and cranial elongation (dolichocrany) in contrast to the facial elongation (dolichopy) and cranial abbreviation (brachycrany) of the horses. The changes of head form in *Dolichorhinus* are shown to be continuous and to result in dolichocephaly and cyptocephaly—that is, bending down of the face upon the cranium, as in the reindeer (*Rangifer*) and the hartebeest (*Bubalis*). The adaptive mechanical significance or selection survival value of these allometrons is sometimes apparent, sometimes obscure.

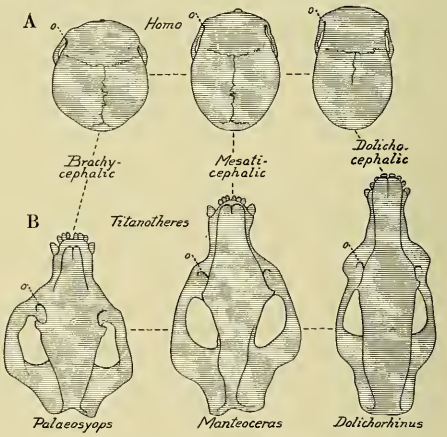


FIGURE 739.—Continuous origin of allometron biocharacters in the cranium and skull of man (A) and of the titanotheres (B)

In reference to man the words brachycephalic, mesaticephalic, and dolichocephalic denote respectively, brachycranial, mesaticranial, and dolichocranial—in other words, they describe the proportions of the cranial cavity. In reference to the titanotheres the same words are used to describe the relative length and breadth of the entire skull. Note especially the relative position of the orbit (o).

TERMINOLOGY INDICATING PROPORTIONS OF THE SKULL AND SKELETON

The general terminology of the changes in the proportion of the skull and postcranial skeleton has been gradually developed in the study of human and com-

[59] The author's chief contributions to the craniometry of the titanotheres and other ungulates are the following: Dolichocephaly and brachycephaly in the lower mammals: Am. Mus. Nat. Hist. Bull., vol. 16, art. 7, pp. 77-89, Feb. 3, 1902; Coincident evolution through rectigradation (third paper): Science, new ser., vol. 27, No. 697, pp. 749-752, May 8, 1908; Skull measurements in man and the hoofed mammals: Science, new ser., vol. 35, No. 902, p. 596, Apr. 12, 1912; Craniometry of the Equidae: Am. Mus. Nat. Hist. Mem., new ser., vol. 1, pt. 3, pp. 57-100, figs. 1-17, June, 1912.

6. Enlargement of the head as a whole=macrocephaly.
   Relative diminution of the head as a whole=microcephaly
7. Elongation of the limbs as a whole=dolichomely.
   Elongation of the feet=dolichopody.
8. Shortening of the limbs as a whole=brachymely.
   Shortening of the feet=brachypody.

PROPORTIONAL EVOLUTION IN THE TYPICAL BRACHYCEPHAL PALAEOSYOPS

As the course of the evolution of *Palaeosyops* from generation to generation is toward solidity, the skulls become progressively larger, the individual parts become more massive, the sagittal and occipital crests become more robust, the linea aspera of muscular origin and insertion becomes more pronounced, the zygomata become more widely arched and thicker in section posteriorly, and the zygomatic flanges become deeper.

syops is partly ancestral or inherited (paleotely), and it partly looks forward (cenotely) to a similar proportional evolution in a certain direction or a sum of proportional changes whose effects are less clearly manifest in lower stages and become more and more evident in higher stages. The harmonic tendency toward progressive weight and brachycephaly is accompanied by the disharmonic tendency in certain changes of proportion.

BRACHYCEPHALIC ALLOMETRONS AFFECT ALL BIOCHARACTERS; HARMONIC

To a certain degree brachycephaly affects every contour, relation, bone, and tooth in the skull. Even in the earliest known species of *Palaeosyops* brachycephaly is the dominant evolutionary trend, although we still find reminiscences of less brachycephalic ancestors, forms more like the mesaticephalic *Limnohyops* and *Telmatherium*. The modes of departure from an ancestral, more generalized type toward the extreme brachycephalic type are apparent in every biocharacter, as shown in the eighteen structural features listed below:[60]

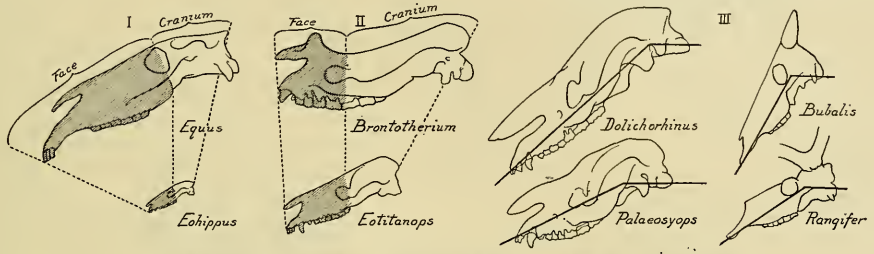


FIGURE 740.—Proportions and flexure of skull in horses and titanotheres

I, Horse proportions: *Equus*, face elongated, cranium abbreviated; *Eohippus*, cranium and face equal. II, Titanothere proportions: *Brontotherium*, face abbreviated, cranium elongated; *Eotitanops*, cranium and face equal. III, Skull flexure (cyptocephaly) in ruminants (*Rangifer*, *Bubalis*) and titanotheres (*Palaeosyops*, brachycephalic; *Dolichorhinus*, dolichocephalic).

CONTRAST BETWEEN EVOLUTION AND GROWTH

The first impression from these modes of change is that in *Palaeosyops* skull evolution is like a continuous growth, as if the skulls found in the higher geologic stages represented extremely long-lived, mature, but not senescent forms of the skulls found in earlier geologic stages. This impression is only partly true. In evolution new proportions develop through the separate rate of change of different biocharacters; consequently evolution is more fully differential than growth.

DIFFERENTIAL (DISHARMONIC) ALLOMETRONS IN PALAEOSYOPS

In the evolution of the genus *Palaeosyops* between the lower and upper Bridger beds (a geologic interval of 1,500 to 2,000 feet) there is an average increase of about 14 per cent in the size of the skull, but this ranges in the different bones of the skull from 8 per cent minimum to 73 per cent maximum. Thus there is a prolonged harmonic evolution toward brachycephaly and a separate differential evolution of biocharacters. Therefore the generic character of *Palaeo-*

1. Ancestral, smaller, mesaticephalic type, only partly known, passes into the progressively larger, more brachycephalic type.
2. Skull as a whole increases in massiveness, showing a more rapid increase in breadth than in length—that is, as 1.5 to 1.
3. Premaxillary symphysis becomes short and rounded.
4. Maxillaries are increasingly abbreviated.
5. The nasals, originally more elongate and obtuse, become more abbreviate and pointed.
6. A smooth, plane forehead develops a prominent forehead convexity.
7. The malar below the orbit deepens with extreme rapidity.
8. The zygomata become more arching and deeper.
9. Postglenoid and post-tympanic processes, originally separate and leaving external auditory meatus open below, become almost united, closing external auditory meatus below.
10. Paroccipital process, distinct at base from post-tympanic process, becomes confluent at the base with post-tympanic process.
11. Basifacial plane, originally more horizontal, becomes displaced downward.
12. Palatines exhibit an abbreviated exposure on the palate.

[60] Other progressive characters are enumerated on p. 257.

13. Foramen ovale approaching foramen lacerum medium.
14. Postcanine diastemata disappearing.
15. Mandibular rami develop a short, triangular coronoid process, condyle elevated, mandible with depressed angle; face of coronoid flattened in front, tending to overhang third inferior molar; rami increasing in depth and thickness; diastema between canines and first premolars disappearing.

attributed to *Palaeosyops* are the expressions of its progressive brachycephaly. These so-called generic characters are based upon the harmonic trend, or direction, of evolution in the skull as a whole with its correlated changes in a large number of biocharacters. Some of the "specific" characters which the

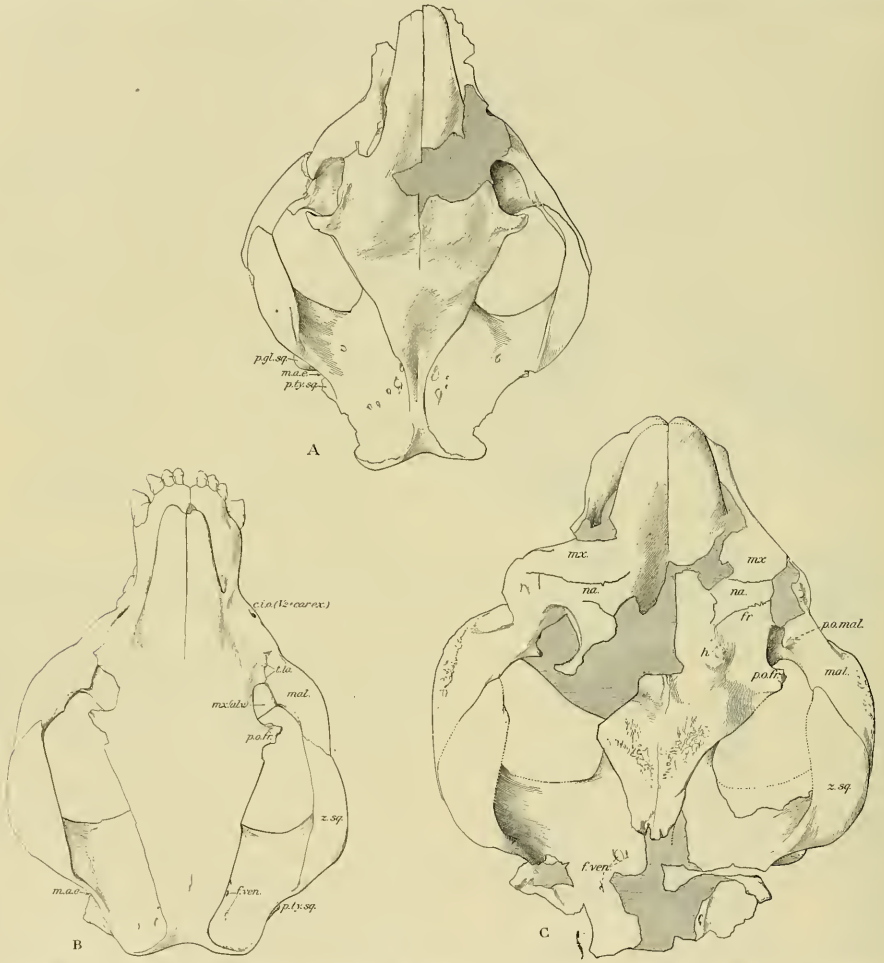


FIGURE 741.—Skulls of three species (probably successive) of *Palaeosyops* from the middle Eocene, Bridger formation

A, *P. major*, level B 3; B, *P. leidyi*, level probably upper C or D; C, *P. robustus*, level probably D.

16. Incisors become more transverse in position; canines stouter and rounder.
17. Molars become broader than long; parastyle robust; robust internal and external cingula.
18. Hypoconulid of m_3 from a subcrescentic form acquires a progressively conic form.

HARMONIC PROPORTION TREND CONSTITUTES THE GENERIC CHARACTER OF PALAEOSYOPS

The chief "generic" characters which Leidy, Cope, Earle, Osborn, and others have from time to time

same authors have attributed to *Palaeosyops* are the successive stages in its progressive brachycephaly. Other specific characters consist of successive rectigradations which are added to the teeth and the skull.

FOURFOLD MODES OF ALLOMETRIC BRACHYCEPHALY

From comparison with the skulls of other mammals we draw four important conclusions in the study of the allometric brachycephaly of the skull of *Palaeosyops* as a whole, namely:

1. *No addition of biocharacters in Palaeosyops.*—In *Palaeosyops* no distinctively new elements or organs are added to the skull through progressive brachycephaly and no characters are lost, but allometrons are established by the abbreviation of some parts and the expansion of conjoining parts. For example, the postglenoid and post-tympanic processes tend to close in the auditory meatus.

2. *Correlation of biocharacters.*—Age and sex both exert a positive divergent influence on all the quantitative characters of the skull, such as massiveness and robustness. Old male skulls are more progressive in form, more prophetic of higher successive stages than young male skulls, and some female skulls are more conservative in form than male skulls. In brachycephalic phyla the females preserve the more mesaticephalic indices of ancestral forms Similar conclusions are summarized by Dr· C. Hart Merriam (1895.1), from his studies on the pocket gophers (Geomyidae), as follows:

> The female generally has the brain case broader and flatter, the zygomata narrower and less angular, the jugal narrower anteriorly, the rostrum and nasals shorter, and the skull as a whole smoother. In other words, the cranium of the female is much less specialized than that of the male and often points suggestively to the stock from which the species was derived. It thus happens in the case of series of species in which the successive forms in the development of a particular type are still extant (as in the *texensis-bursarius* series) that the female resembles the male of the species next below in the line of descent more than the male of her own species.

Concerning the influence of age and musculature the same author observes (op. cit., p. 32):

> Fundamental characters are based on structures and relations that enter into the ground plan of the skull and are of high morphologic weight; superficial characters are the result of special adaptations and particular muscular strains and are of little value except as affording recognition marks for species and in some instances for genera also. The fundamental structures are mostly hidden, comprising the floor of the brain case, the craniofacial axis, and the turbinated bones.

Thus young jaws of the species of *Palaeosyops* and *Limnohyops* are more similar to each other than old jaws.

3. *Remoteness of zoologic affinity (family, supragenerie, and generic).*—Such affinity apparently exerts little or no controlling influence on the brachycephalic evolution of *Palaeosyops*, because we observe that other related generic forms (*Limnohyops, Telmatherium*) are evolving differently along their own lines.

4. *Closeness of zoologic affinity (generic, specific, varietal).*—These relationships exert a positive controlling influence because of the kinship of (1) a common progressive brachycephalic tendency, (2) the kinship of similar habit and habitat, and (3) the kinship of a similar incidence of competition and selection

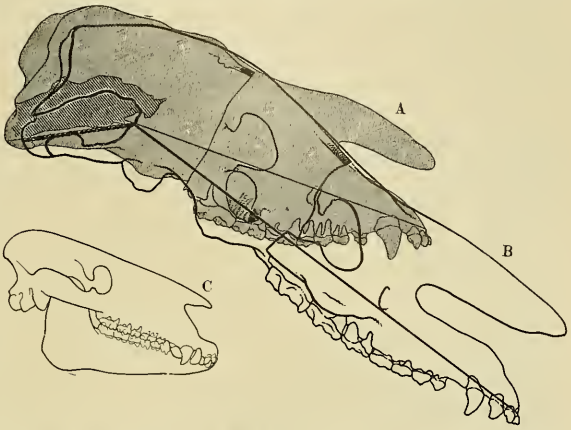


FIGURE 742.—Outlines of skulls of *Palaeosyops, Dolichorhinus*, and *Eotitanops*, illustrating the evolution of brachycephalic and dolichocephalic types

A, Brachycephalic skull of *P. leidyi* (shaded), superposed upon B, dolichocephalic skull of *D. hyognathus* (heavy outline); C, hypothetic outline of the skull of *E. gregoryi*, drawn to the same scale as A and B. This illustration shows the contrasts produced in the evolution of brachycephaly, dolichocephaly, and cyptocephaly from the primitive mesaticephaly of *Eotitanops*.

DIFFERENTIAL ALLOMETRONS OF SPECIFIC VALUE

While the skull as a whole is increasingly brachycephalic the differential rate of increase in its separate parts furnishes an important share of the material which paleontologists have seized upon in the systematic description of "species." This is shown in the careful analysis of the measurements given in the following table:

Differential measurements, in millimeters, in seventeen dental and cranial characters of skulls transitional between Palaeosyops major, P. leidyi, and P. robustus

[All from the Bridger formation]

	P. major, Am. Mus. 12182, level B 3, age 1	Transitional skull, Am. Mus. 12185, level C 3, age 2	P. leidyi, Am. Mus. 1516, level C or D, age 3	P. leidyi, Am. Mus. 1544, level C or D, age 6	P. robustus?, Am. Mus. 1581, level C or D, age 5	P. robustus, Am. Mus. 11678, level D 4, age 4	P. robustus, Am. Mus. 1580, level C or D, age 5	P. robustus, Princeton Mus. 10282 b, level C or D, age 4	Percentage increments, P. major to P. leidyi	Comparative increments (4 per cent taken as unit), P. major to P. leidyi	Percentage increments, P. leidyi to P. robustus	Comparative increments (4 per cent taken as unit), P. leidyi to P. robustus	Percentage increments, P. major to P. robustus	Comparative increments (12 per cent taken as unit), P. major to P. robustus
1. P^4, transverse	24	----	25	25	----	----	a28	27	4	1	8	2	12	1
2. P^2–m^3, anteroposterior	148	151	151	158	----	----	a170		2. 4	. 6	11	2. 7	14	1. 1
3. M^1–m^3, anteroposterior	94	----	102	100	----	94	a103	100	6. 4	1. 6	3	. 75	9	. 75
4. Tip of premaxillaries to condyles	390	----	413	415	----	----	a440	----	5. 8	1. 7	6. 5	1. 6	11	1
5. Cranium, postorbital process of frontals to condyles (projected)	183	----	193	199	----	----	a206	----	5. 6	1. 4	3. 1	. 7	12	1
6. Face, postorbital process, frontals to premaxillaries	207	----	220	216	----	----	a234	----	4. 3 or 6. 2	1 or 1. 5	6. 3	1. 5	13	1
7. Breadth across zygomata	a288	----	a285	310	----	a325	a340	----	13	3. 2	15	3. 7	18	1. 5
8. Breadth across postglenoid	----	----	181	195	----	224	----	----	----	----	16	4	----	----
9. Breadth across post-tympanic	a156	----	163	166	----	a172	----	----	----	----	5. 5	1. 4	----	----
10. Maximum width, one condyle	52	----	56	57	----	58	a61	----	6. 8	1. 7	9. 7	2. 4	14	1. 1
11. Depth, midzygoma	----	53	53	62	----	60	----	----	----	----	17	4	----	----
12. Depth, malar below postorbital process malar	40	50	55	58	59	59	70	a70	38	9	26	6. 5	73	6
13. Free length of nasals	86	----	92	92	103	----	a108	----	8	2	15	3. 7	25	2
14. Postorbital process of frontal to tip of nasals	180	----	189	189	----	----	a208	----	5	1. 2	11	2. 7	15. 5	1. 2
15. Postorbital process of frontal to nasal canthus	91	----	101	101	108	----	----	----	12	3?	7	1. 7	20	1. 6
16. Postorbital process of frontal to tip of occiput	196	----	208	208	----	----	----	----	5	1. 2	----	----	----	----
17. Tip of nasals to tip of frontal convexity	240	----	240?	240	240	----	a250	----	0	0	4	1	4	. 33

a Estimated.

On account of the breaks in the phyletic series and the effects of distortion the results presented in the above *Palaeosyops* table are approximations. They would have been much more striking had it been possible to compare completely the earliest, smallest known form, *P. paludosus*, with one of the latest and largest forms, *P. grangeri*, and had all the skulls been free from distortion. In this table are compared only the three intermediate stages, *P. major*, *P. leidyi*, *P. robustus*, from which the following principal generalizations may be made.

HARMONIC ALLOMETRY EXCEPTIONAL

Of the 17 characters mentioned in the above table 2 only are harmonic, giving exactly the same percentages of increase. Other characters which show near approximations to harmonic increase are (4) the length of the skull, (2) the length of the grinding teeth, (1) the breadth of the fourth premolar, (10) the width of the occipital condyle. These nearly harmonic increments range from 11 to 14 per cent.

The skull increases 7 per cent faster in breadth than in length, the breadth increment being 1.6 times the length increment. From *P. major* to *P. robustus* the skull increases in length 50 millimeters, or 11 per cent; it increases in breadth 57 millimeters, or 18 per cent.

Cranial and facial increments are subequal. The gain in the length of the preorbital region is 12 per cent; the gain in the postorbital region is 13 per cent. Thus in *Palaeosyops* the face and the cranium increase at approximately equal rates, whereas in most other titanotheres the cranium increases more rapidly than the face. For example, in *Dolichorhinus* (as compared with *Mesatirhinus*) during a given period the face increases 26 per cent and the cranium 38 per cent.

The greatest gain differentially is in the breadth of the masseteric muscle area of the zygomata. On comparing a young adult specimen of *P. major* with an aged specimen of *P. robustus* we observe a gain of 73 per cent in the depth of the malar below the orbit.

When we compare these percentages with those based on similar measurements of skulls of specimens of other genera we again establish as the distinct generic character of *Palaeosyops* that it is a genus characterized by certain definite (that is, brachy-

cephalic) and highly differential rates of evolution in different parts of its skull and teeth. Although progressive brachycephaly is the chief harmonic trend of development, this harmonic trend affects every bone in different degree.

DOLICHORHINUS: ADAPTATION OF THE LENGTHENED HEAD TO THE SUPPOSED HABIT OF GRAZING

In the *Dolichorhinus* phylum (Dolichorhininae) we are afforded a unique opportunity of studying the allometry that transforms a mesaticephalic skull (*Mesatirhinus petersoni*) into a dolichocephalic skull (*Dolichorhinus hyognathus*) with a strong tendency to cyptocephaly. The comparison between the older and newer forms is not absolutely exact because we can not yet demonstrate positively that *Dolichorhinus* was directly descended from *Mesatirhinus*, but we are certain that the changes came about through a general lengthening of the skull with a relative narrowing; moreover, that this is the result of a differential evolution in which some bones grow much more rapidly than others. At least part of these changes are apparently correlated with adaptation to the habit of grazing.

A comparison of *Dolichorhinus* and *Palaeosyops* discloses the following eight features of *Dolichorhinus:* (1) There is a general dolichocephalic increment of 33 per cent; (2) harmonic increment is rare; (3) increment in length greatly exceeds increment in breadth; (4) cranial increment (dolichocrany) exceeds facial increment (dolichopy); (5) the increment in breadth is the minimum; (6) head bending (cyptocephaly) is due to the increment in the length of the roof bones of the skull in excess of those of the basicranial line; (7) the increment of the grinding series and of the cranium is harmonic; (8) the increment of different members of the grinding series is differential, disharmonic.

DOLICHOCEPHALIC INCREMENTS OF MESATIRHINUS AND DOLICHORHINUS

As *Mesatirhinus petersoni* is itself a dolichocephalic form these changes are not so marked as they would be were we to compare *Dolichorhinus hyognathus* with its unknown mesaticephalic ancestors, yet we discover very marked allometry. Partly owing to the crushed condition of the skulls a very high degree of accuracy can not be claimed for the percentages in the table, although they are based on averages obtained from a very large number of measurements. The two chief peculiarities of *Dolichorhinus hyognathus* as compared with *Mesatirhinus petersoni* are the excessive length of the skull as a whole and the convexity (cyptocephaly) of the cranium.

The cyptocephaly of the skull was brought about by more rapid evolution of the top or upper bones than of the bottom, the basicranial and palatal bones. The total skull measurement (cranium to face) from the tip of the nasals to the tip of the occiput along a dorsal line increased 44 per cent, whereas the measurement along the inferior line, premaxillaries to condyles, increased only 33 per cent. The top of the cranium proper (postorbital process, frontals to tip of occiput) shows an increase of 40 per cent, whereas the corresponding measurement of the basal line (original boundary of posterior nares to posterior face of condyles) shows an increase of only 30 per cent. The basis of the cranium, the cranio-facial angle, has been produced downward with relation to the basis of the face from 157° (or 23°) in *M. petersoni* and 136° (or 44°) in *D. hyognathus*—that is, through 21°.

The skull as a whole, premaxillaries to condyles, and the cheek teeth as a whole, p^1–m^3, increased about equally in length (33 per cent). A similar equal increase of the skull and cheek teeth also marks the progressive dolichocephaly of the Oligocene genus *Menodus*. The cranium lengthens more rapidly than the face. The proportional evolution of the cranium and face can best be measured on a horizontal line from the tip of the premaxillary to the condyle, by projecting on this line the tip of the postorbital process of the frontal. The face increment (26 per cent) is thus seen to be 12 per cent less than the cranium increment (38 per cent) and 7 per cent less than the increment of the skull as a whole (33 per cent). The region of the greatest elongation of the cranium is that between the hinder border of m^3 and the foramen ovale, which increases 54 per cent. In front of and behind this region the increments in length are less, as shown in the series of detailed comparative measurements below. It is in this greatly stretched region that many anatomical peculiarities, such as the extremely elongate posterior nares and the protrusion of the ethmoturbinal, the secondary palate, are noted.

Other features of differential evolution in length are as follows: The premaxillaries and the postcanine diastemata have lengthened faster (increment 44 per cent) than the skull as a whole (33 per cent). The free portion of the nasals has increased 55 per cent, and the nasals as a whole have increased 70 per cent as compared with the skull as a whole (33 per cent). The zygomata have increased 44 per cent, or much more than the skull as a whole (33 per cent). There is a marked forward displacement of the postglenoid process, the distance between the postglenoid and post-tympanic processes having increased 55 per cent, whereas the corresponding distance between the foramen ovale and foramen condylare has increased only 34 per cent. As a result of this forward displacement of the postglenoid process, the external auditory meatus has been rotated forward from an angle of 78° in *M. petersoni* to a corresponding angle of 53° in *D. hyognathus*. The anteroposterior diameter or opening of the external auditory meatus has

received the enormous increment of 79 per cent, which may be contrasted with the actual closure of this same region in the brachycephalic *Palaeosyops*.

SLOW BUT DIFFERENTIAL EVOLUTION IN BREADTH OF SKULL OF DOLICHORHINUS

While the skull of *Dolichorhinus* was rapidly elongating (increment 33 per cent) it was much more slowly evolving in breadth (increment 9 to 15 per cent). Thus the disparity between the length and breadth was constantly increasing, as shown in the following comparisons: (1) The transverse measurement across the zygomata increased 15 per cent, or less than one-half the increment in length of the skull (33 per cent). Similarly, the breadth across the postglenoid and post-tympanic processes increased only 13 per cent. (2) The space across the infraorbital shelves increased only 9 per cent, partly because these shelves were already relatively broad in *M. petersoni*. (3) Consistent with the bracing of this long and narrow skull we observe that the occipital condyles widen much more rapidly than the remainder of the skull, the increment being 28 per cent. (4) Similarly, the occiput increased in breadth 68 per cent in order to provide a large surface of attachment for the cervical and cephalohumeral muscles. The fact that the occiput increased in height only 20 per cent indicates that the horns were used in an obliquely lateral rather than in a tossing motion. (5) The transverse measurement across the horn region shows the relatively high increment of 35 per cent, while the transverse measurement across the postorbital processes of the frontals increased 23 per cent. (6) A noteworthy fact is that the palatal space between the anterior premolars receives the large increment of 45 per cent. This broadening of the palate anteriorly would allow greater space for the incoming food.

DIFFERENTIAL EVOLUTION IN THE GRINDING TEETH OF DOLICHORHINUS

It is a striking fact that the teeth as a whole increased in length at practically the same rate as the skull as a whole, namely, 32 per cent. A second fact of great interest is that the dental series lengthens much more rapidly than the individual teeth increase in width, the transverse increment of the teeth being but 17 per cent while the total longitudinal increment is 32 per cent. The teeth thus share the general elongation of the skull. The grinding areas of the cheek teeth as a whole become larger. Measuring the grinding areas by the sum of the rectangles circumscribed by each tooth in the series we find that the grinders of *D. hyognathus* have received an increment of 68 per cent over those of *M. petersoni*. This increase is differential, however, because the grinding area of the premolars has increased only 41 per cent as against 76 per cent increase in the true molars. This is the reverse of what occurs in the horse, in which the premolar increment is greater than the molar increment.

The increment of the total grinding area of the crowns among the individual teeth is distributed as follows: P^1, a very slight increment in size; p^2, an increment in grinding area of 48 per cent; p^{3-4}, an increment in grinding area of 36 per cent; true molars, m^{1-3}, an increment in grinding area of 80 per cent. Thus the true molars received by far the greatest increment.

CONTRASTS OF DIFFERENTIAL EVOLUTION IN BRACHYCEPHALIC AND DOLICHOCEPHALIC SKULLS

The net results of these increments in length and width may be summarized as follows:

Percentages of increase in size of skull and teeth of Dolichorhinus and Palaeosyops

	Dolichocephaly (Dolichorhinus)	Brachycephaly (Palaeosyops)
Increment in length:		
1. Entire skull, premaxillaries to condyles	33	11
2. Top of skull, tip of nasals to tip of occiput	44	------
3. Cranium proper, postorbital region	38	13
4. Face proper, preorbital region	26	12
5. Premaxillaries, anterior part of face	44	------
6. Nasals, measured from above	70	------
Increment in breadth:		
7. Zygomatic arches	15	18
8. Postglenoid and post-tympanic processes	13	------
9. Across infraorbital shelves	9	------
10. Across occipital condyles	28	------
11. Across occiput	68	------
12. Across horn swellings	35	------
Elongation of grinding teeth:		
13. Total	32	14
14. Premolar series	------	0
15. True molar series	------	9

SUMMARY OF HARMONIC AND DIFFERENTIAL ALLOMETRONS IN THE SKULLS AND FEET AND AN INTERPRETATION OF THE PHYLOGENY OF THE TITANOTHERES

By W. K. Gregory

HISTORY OF RESEARCH

The first step toward the discovery of the allometric principle was the analysis of dolichocephaly and brachycephaly in the titanotheres by Osborn in 1902 (1902.208). At that time it seems to have been thought that the tendencies toward the long-headed and short-headed forms were mutually exclusive and that their divergent mass effects indicated a very ancient separation between the corresponding genera. It was also apparently assumed (Osborn, 1902.207) that the tendencies acted more or less uniformly on all parts of the skull.

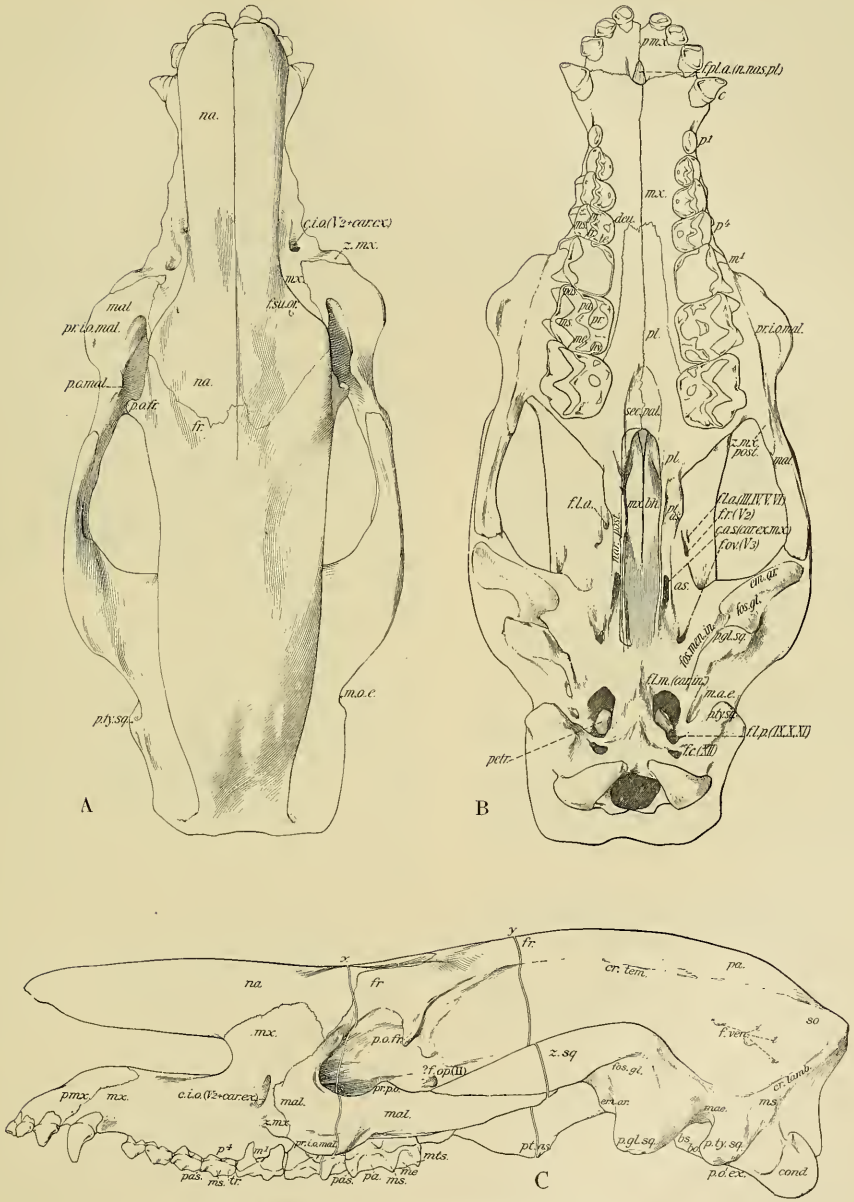


FIGURE 743.—Skull of *Dolichorhinus hyognathus*

Am. Mus. 1851 (type of "*Telmatotherium cornutum*"). Top (A), palatal (B), and left side (C) views.

In 1904, by a study of the progressive percentages of increments in the skulls of *Palaeosyops* and *Dolichorhinus* for this monograph, Gregory was able to establish the principle of differential as opposed to harmonic dolichocephaly. In 1907 Osborn, in considering the nearness of affinity of the subdolichocephalic *Mesatirhinus* to the relatively broad-skulled *Manteoceras*, concluded that broadening and lengthening were "quantitative" characters, which were largely independent of remote hereditary control. In 1908 Gregory's studies indicated that the dolichocephalic *Menodus* and the brachycephalic *Brontops*, together with the intermediate genus *Allops*, constituted a separate group, the menodontine, in contrast to the brontotheriine group, including the relatively long-skulled *Brontotherium* and the broad-skulled *Megacerops*.

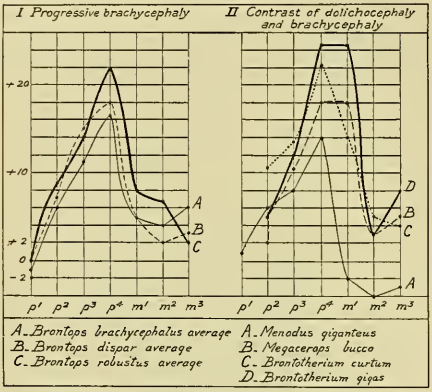


FIGURE 744.—Differences in the proportions of premolars and molars corresponding to differences in the proportions of the skull

Progressive brachycephaly: Graph I shows numerical excess of transverse over anteroposterior diameters of the upper premolars and molars in successive stages of the progressively brachycephalic *Brontops* phylum.

Contrast of dolichocephaly and brachycephaly: Graph II shows contrasts in the proportions of the upper premolars and molars between dolichocephalic (A) and brachycephalic titanotheres (B, C, D). The dolichocephalic form (A) has relatively narrow premolars and positively narrow molars, in which the transverse becomes less than the anteroposterior diameter.

In a study of reversal in the proportions of the feet, Gregory in 1910 (1910.1) adduced evidence to show that the broad-footed genera *Palaeosyops*, *Manteoceras*, *Megacerops*, *Brontotherium* had been derived from narrow-footed stem forms and that their broad magnum had been derived from a narrow magnum having a wedge-shaped lower end, much like that of *Eotitanops*.

By a close study of the Eocene titanotheres in the spring of 1914 Osborn and Gregory discovered a principle that may afford a key to the phylogeny of the titanotheres: Differential lengthening and broadening of all parts of the skull and feet have acted either simultaneously or in combination at different rates in the several phyla.

APPLICATION OF THE PROPORTIONAL REVERSAL PRINCIPLE TO THE TITANOTHERES

Eotitanops.—Eotitanops borealis is dolichocephalic. The details of the dentition and infraorbital, malar, and other characters of the skull show that it is structurally ancestral, or nearly so, to the progressively brachycephalic *Limnohyops* and *Palaeosyops*. This fact favors the view that the narrow-footed *Eotitanops* [61] gave rise to the broad-footed *Palaeosyops*.

Telmatherium.—Telmatherium unquestionably resembles *Manteoceras* in some characters, the Palaeosyopinae in others. A close study of the skull and dentition of *T. cultridens* shows no feature inconsistent with remote derivation from a mesaticephalic species allied generically to *Eotitanops borealis*. *Telmatherium ultimum* conserved the mesaticephalic features of the basicranial region, but the middle part of the skull, like that in all Uinta Basin forms, had already undergone considerable elongation. The premolar series, p^2–p^4, as shown by percentage ratios, is relatively longer in *T. cultridens* than in *Eotitanops;* but in *T. ultimum* the molars have lengthened so much that the premolar series is again relatively short. In this species, however, the molars have also broadened decidedly, so that they are very large and somewhat broad. Here, then, was a combination of differential broadening and lengthening.

Manteoceras.—As compared with the very primitive and ancient titanothere *Eotitanops*, the hypothetical ancestors of *Manteoceras* in the Wind River were also mesaticephalic and probably allied to the forms that are ancestral to *Telmatherium* and to *Palaeosyops*. The Bridger *Manteoceras* shows a broadening of all parts, as well as a lengthening of the middle portion of the skull; the grinding series also shows a slight broadening and a relative increase in size. But in the Uinta C stage (*M. uintensis* Douglass) a marked dolichocephalic tendency has supervened, affecting especially the postcanine diastema and the length of the premolars and of the first and second molars. In the feet *Manteoceras manteoceras* shows a marked secondary broadening of the slender-footed type and is clearly allied to the narrow-footed *Mesatirhinus*.

Protitanotherium.—Protitanotherium, to judge from the resemblances in the dentition and skull to *Manteoceras uintensis*, was possibly a derivative of some earlier species of *Manteoceras*. In common with all other upper Eocene and Oligocene titanotheres *Protitanotherium* had probably suffered an elongation of the middle portion of the skull, but in addition to and superseding this, a strong brachycephalic tendency had set in which, to judge from the front part of the skull and dentition, had brought *Protitanotherium* near to the stem of *Brontops*.

[61] The fifth digit of *E. borealis* is perhaps not reduced past hope of subsequent increase. It is broken off in the type.

Brontops.—The elongation of the midcranium having been effected, *Brontops* began to develop buccal brachycephaly and finally carried it to an extreme in *B. robustus* and *"Diploclonus" amplus.*

Allops.—*Allops* lengthened the skull, and especially the molar series, but also showed some brachycephalic tendency. Its transitional character between *Brontops* and *Menodus* points to the convergence of those two lines at a not very distant date, perhaps during some stage of the upper Eocene.

Menodus.—*Menodus* was probably not derived from *Telmatherium*, for the incisors of that genus progressively increase rather than decrease in size; also the close alliance of *Menodus* and *Brontops* points rather to the possible derivation of *Menodus* from some subdolichocephalic form of *Manteoceras*, like *M. wintensis*, yet retaining the sharper-edged canines of certain species of Bridger *Manteoceras*. At any rate, *Menodus* carried dolichocephaly to an extreme, yet shows a slow progressive broadening across the zygomata (*M. heloceras* to *M. giganteus*).

Mesatirhinus.—The skull of *Mesatirhinus* as compared with that of *Eotitanops* had already lengthened all the parts. This dolichocephalic tendency became

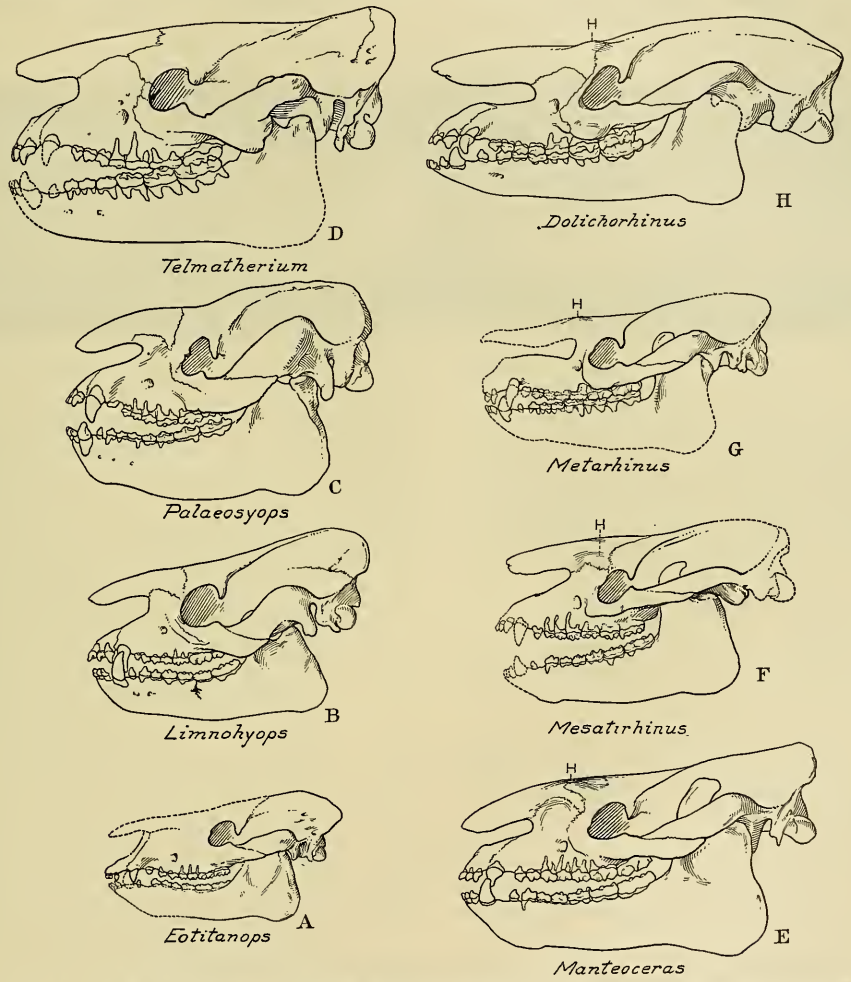


FIGURE 745.—Skulls of Eocene titanotheres, showing changes in proportion and in development of horns

Hornless series: A, *Eotitanops borealis;* B, *Limnohyops priscus;* C, *Palaeosyops leidyi;* D, *Telmatherium ultimum.*
Precociously horned series: E, *Manteoceras manteoceras;* F, *Mesatirhinus petersoni;* G, *Metarhinus carlei;* H, *Dolichorhinus hyognathus.*

very pronounced in the most advanced members of *Mesatirhinus petersoni* and culminated not only in the long-skulled *Dolichorhinus* but even more in the allied *Sphenocoelus*. The feet of the *Mesatirhinus* were derived from those of *Eotitanops* by a slight relative broadening of the carpals, tarsals, and metapodials. *Dolichorhinus*, contrary to former views, was not dolichopodal but so far as the evidence shows was subbrachypodal, the foot proportions being

markedly hypsodont and had very flat ectolophs. Certain specimens of *Metarhinus fluviatilis* had a lower jaw like that of a minute *Megacerops*. Not all metarhines were small; a lower jaw (Am. Mus. 1859) shows, in fact, clear indications of a species of *Metarhinus* larger than *R. diploconus*.

Rhadinorhinus.—As elsewhere fully shown, *Rhadinorhinus* in many characters foreshadows the stem form of the Brontotheriinae; *R. diploconus* especially is

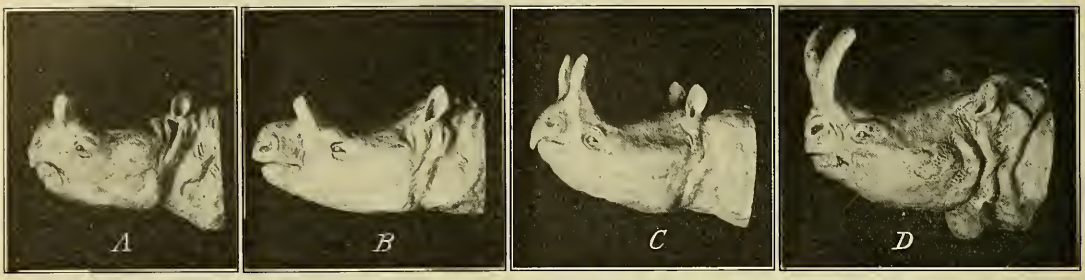


FIGURE 746.—Models of heads of Oligocene titanotheres showing general proportions, especially form of lip and horns
A, *Brontops* (brachycephalic); *B*, *Menodus* (dolichocephalic); *C*, *Megacerops* (hyperbrachycephalic); *D*, *Brontotherium* (brachycephalic).

derived by moderate broadening and little or no lengthening from those of forms like *Mesatirhinus*.

Metarhinus.—*Metarhinus* is undoubtedly a near ally of *Mesatirhinus* and even parallels *Dolichorhinus* very closely in many characters of the dentition and skull; but in *Metarhinus* the basicranial and midcranial regions, after becoming subdolichocephalic,

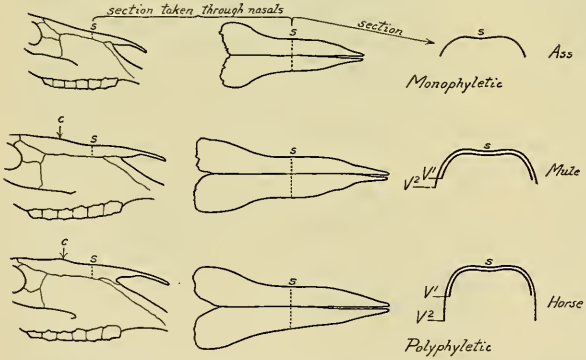


FIGURE 747.—Separability and imperfect blending of allometric biocharacters in the facial bones of the horse (*Equus caballus*, ♀), ass (*E. asinus*, ♂), and mule

Left column: Bones of the side of the face, preorbital region. *c*, The bump on the forehead of the horse and mule not observed in the ass. *s*, The point at which the section of the nasals is taken.
Middle column: Nasal bones of the horse, ass, and mule viewed from above, showing that the nasal bones of the mule closely approximate in proportions those of the horse. *s*, Point at which the transverse section is taken.
Right column: Transverse section of the nasal bones of the horse, ass, and mule at the point indicated by *s*, showing the shallow nasal bones of the ass, a pure monophyletic type; the variability (V^1–V^2) in the depth of the nasals in the horse, which is due to the fact that the domestic *E. caballus* is a type derived by interbreeding of several distinct races, and the intermediate depth of the nasals in the mule.

ceased to elongate, and the elongation of the face was retarded at an early period. The molars became distinguished by the short, upturned face, the narrow preorbital region, the rounded malar-lacrimal bar, the saddle-shaped skull top, the narrow, pointed nasals, and many other brontotheriine characters. The mingling of dolichocephalic and brachycephalic characters in *R. diploconus* foreshadows a similar mingling in *Brontotherium*, which has an elongate skull and a short face.

Possible bearings of the facts stated on phylogeny.—Assuming provisionally the correctness of this view, the history of the brontotheriine skull may have been as follows:

1. A mesaticephalic member of *Eotitanops* gave rise to the subdolichocephalic *Rhadinorhinus*, in which, however, the face was not lengthened. The middle and basicranial parts of the skull continued to lengthen, but perhaps in late upper Eocene time the tendency toward brachycephaly gathered momentum and resulted in the broad zygomata, the broad frontals, and the widely spreading horns of *Brontotherium*. The molars in the *Rhadinorhinus* stage were relatively long anteroposteriorly, but later they widened rapidly with the skull. The premolars also widened, and the incipient tetartocones were carried to an extreme in *Brontotherium*.

2. In the allied *Megacerops* the broadening tendency early attained predominance, resulting in a broad, short-faced skull.

3. The changing proportions of the feet in the same phylum were hypothetically as follows: The narrow foot of *Eotitanops* gave rise, chiefly by an increase in size but also by some degree of broadening, to the narrow foot of *Rhadinorhinus;* the narrow foot of *Rhadinorhinus* may

have broadened out, especially the magnum and astragalus, into the broad foot of *Brontotherium*.

4. These examples, for which detailed evidence is given elsewhere, thus illustrate the supposed intermingling and alternate triumph of tendencies toward lengthening and broadening of the parts in the various phyla of titanotheres.

IRREVERSIBLE AND REVERSIBLE EVOLUTION OF ALLOMETRONS

The marked trend in certain directions which we have termed "progressive brachycephaly," "progressive dolichocephaly," and "cyptocephaly" in some cases runs to an extreme, so that the skull reaches a limit of broadening, of lengthening, or of bending that is apparently an inadaptive extreme—an assertion as to adaptation, however, which may be a matter of opinion or of theory rather than a statement of established fact. The broadening and lengthening tendency seems certainly to be cumulative in successive generations, affecting the skull as a whole.

Such a tendency, however, does not apply to parts of skulls in which reversible allometry is observed. On comparing the skull of *Brontotherium leidyi* with those of all lower Eocene Perissodactyla we see at once that there has been a marked lengthening of the cranium proper. On comparing the skull of this form with that of its late successor *B. platyceras* we see that the progressive lengthening has either ceased or has been overshadowed by a marked broadening. Here, then, is an example of lengthening that has been superseded by broadening. A similar process is seen in *Brontops*. Although *Brontops brachycephalus* has a relatively longer cranium proper than the primitive Perissodactyla, the lengthening was later overshadowed by the broadening, both of the skull top and of the zygomata, that culminates in *B. robustus* and *"Diploclonus" amplus*.

The observation that broadening of the skull or certain of its parts sometimes succeeds lengthening is paralleled in the evolution of the feet, where graviportal (weight-bearing) proportions often succeed subcursorial (slender) proportions. This reversible mode of evolution in proportions is of very wide application in the descent of the perissodactyls and other ungulates. Once admitted as a working hypothesis it clears up many hitherto confused problems—the structurally ancestral position of the light-limbed *Hyrachyus* to the heavy-limbed amynodonts and rhinoceroses, of the narrow-skulled, light-footed *Eotitanops* to *Palaeosyops* and perhaps to *Telmatherium*, of the light-footed *Mesatirhinus* to the relatively broad-footed *Dolichorhinus*. If the principle is valid that in graviportal types broadening succeeds lengthening, then there is less difficulty in deriving the broad-footed Oligocene titanotheres with their very broad magnum from the more narrow-footed Eocene types with a narrow (that is, primitive perissodactyl) magnum. (See Gregory, 1910.1, pp. 386, 392–394, 450.)

SEPARABILITY AND CORRELATION OF BIOCHARACTERS

SEPARABILITY OF ALLOMETRONS IN HEREDITY

The above-described differential modes of evolution in the titanotheres furnish presumptive evidence of the germinal separability of allometrons in their velocities of change as biocharacters. The fact that every allometron, like every rectigradation, has a more or less distinctive time of appearance and velocity of change shows that it is also connected with separable germinal genes. This conclusion is confirmed by hybridization in recent mammals.

The central idea of Mendel's discovery is that when two contrasting tendencies (such as dolichocephaly and brachycephaly) enter a hybrid, one from each parent, they separate in the germ cells of the hybrid, so that some of the germ cells are purely dolichocephalic and others are purely brachycephalic, like those of the original parents. Chance meetings of these germ cells give rise to ratios characteristic of Mendelian heredity.

The very important question whether the "broad heads" and the "long heads" as allometric biocharacters have a germinal separability like that of the "tallness" or the "shortness" observed by Mendel in his classic experiments on the pea plant can not be determined in the titanotheres but can be inferred from crosses between "long heads" and "medium heads" in the related horse family, the Equidae. Here, as pointed out by Osborn (1912.372, pp. 177–190), the dolichocephalic skull of *Equus caballus*, when crossed with the relatively mesaticephalic skull of *E. asinus*, gives in the mule a dolichocephalic skull and not an intermediate, blended form.

In crossing the female horse with the male ass it is seen that the skull of the resulting mule has the dominant dolichocephalic proportions of the horse, with slight blending or intermediate proportions of certain bones (like the lacrimal) between the forms observed in the horse and ass.

Careful comparison of the proportion indices in the hybrid mule proves that it inherits from its mother, the horse, very closely the following:

1. Its cephalic index; a long, narrow skull as a whole.
2. Its diastema index; a long diastema, or space for the bit.
3. Its craniofacial index; a relatively short cranium and a very long face.
4. Its orbital index; a long, oval orbit.
5. Its molar index; a relatively long and narrow set of grinding teeth.
6. Its occiput-vertex angle index; a vertically placed occiput. The ass has a much more ancient type of skull than the horse.

Thus the proportions of the horse skull acquired through a long process of allometric evolution prove to be separable biocharacters in the germ. This also proves (Osborn, 1912.372) that proportional characters, although evolving continuously, may exhibit the same germinal separability as the suddenly appearing saltations and mutations of De Vries. Out of 28 characters that were carefully compared in the skull and the teeth of the horse, the ass, and the mule 18 found in the mule are obviously derived either from one parent or the other and show very slight tendency to blend, whereas 10 characters show a distinct tendency to blend.

Yet, so far as our observation shows, rectigradations are more decidedly and distinctly separable in the germ than allometrons.

CORRELATION, COORDINATION; COMPENSATION OF RECTIGRADATIONS AND ALLOMETRONS

In the evolution of rectigradations and allometrons all the biocharacters are harmoniously adjusted to serve the organism as a whole. The adjustments are of six different kinds, as follows:

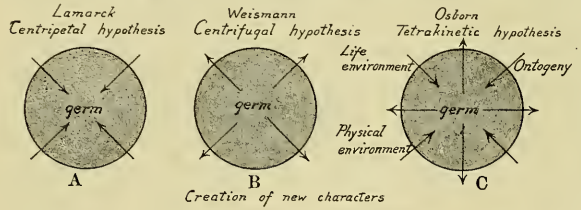


FIGURE 748.—Contrasts between the hypotheses of Lamarck (A), Weismann (B), and Osborn (C) regarding the causes of evolution

The Lamarckian conception of causes is chiefly external, centripetal; the Darwin-Weismann conception of causes is chiefly internal, centrifugal; the tetrakinetic hypothesis is chiefly internal-external, or both centripetal and centrifugal. The balance of existing evidence is in favor of B, the centrifugal hypothesis, since the tetrakinetic theory rests only upon inference from the observed modes of evolution rather than upon actual observation of the external, centripetal origin of any single somatic character.

1. Mechanical correlation of the rectigradations and allometrons in the upper and lower grinding teeth. The reason for this continuous and perfect adjustment is perhaps the most difficult to comprehend in the whole range of titanothere evolution.

2. Mechanical correlation of the developing horns, head, shoulders, and entire locomotor skeleton, with the use of the horns as offensive and defensive structures, with the use of the lips and grinding teeth in the prehension and comminution of food, with the development of the limbs, partly for offense and defense, partly for locomotion. In this general correlation the evolution of various allometrons and rectigradations is continuously and perfectly adjusted.

3. Proportion compensation, a mode of correlation and coordination, by which the development of one character is effected through the sacrifice of another, such as the development of the horns at the expense of the nasal bones. Such compensation correlation is comparatively rare in the titanotheres in contrast with other quadrupeds.

4. Sex correlation or linkage with male or female sex of proportion biocharacters and to a less extent of rectigradation biocharacters, as in the size of the canine teeth, the size of the horns, the proportions of the skull, the varying velocities of ontogenetic and phylogenetic changes in the dentition and all parts of the skeleton, the brachycephaly of males and mesaticephaly of females of the same species.

5. Germinal correlation, by which titanotheres of common ancestry exhibit similar evolutionary tendencies, as in progressive brachycephaly and dolichocephaly, acceleration and retardation.

6. Psychic correlation, as of the horns, with psychic predisposition to use the horns, as explained above in a consideration of ontogenesis of the horns in cattle.

The accompanying diagram (fig. 748) represents crudely the extreme contrasts between the Lamarckian, the Darwinian, and the tetrakinetic points of view.

THEORETIC CAUSES OF THE EVOLUTION OF NEW CHARACTERS AND NEW PROPORTIONS

THEORIES ADVANCED TO EXPLAIN THE ORIGIN OF RECTIGRADATIONS AND ALLOMETRONS

Having compared some of the modes of the evolution of the titanotheres with those of the evolution of other mammals, we may now consider theories that have been advanced to explain the two kinds of evolution upon which our attention is here centered—by rectigradations and by allometrons. Setting aside as unscientific all ideas of "vitalism" and "internal perfecting tendencies," we may group all modern theories of the evolution of form and function under three heads, as follows:

1. External initiation and causation (Lamarckism); modifications of the environment and of the soma. Modifications introduced by change of environment and change of habit are in some manner impressed upon the germ, so that they reappear more or less fully developed in offspring. This idea is inherent in all theories of "direct action of environment" and "inheritance of acquired characters," as developed by Buffon, Lamarck, Spencer, Cope, and others. This general interpretation may be referred to as the Lamarckian.

Evidence: According to this theory germinal variations should be found to originate, to follow, and to correspond closely with individual somatic modifications. They should be orthogenetic and should invariably be followed by similar changes inherited in the bodies of descendants.

2. Internal initiation and causation (Darwinism): Chance, accidental, fortuitous heritable variations in the germ, minor germinal saltations, germinal mutations (De Vries), predispositions that give rise to favorable or unfavorable alterations of character and function, of survival value, accumulated under the action of natural selection or natural elimination. This is the pure Darwinian interpretation.

Evidence: According to this theory variations should originate no adaptive tendency except through the cumulative action of selection in a given direction; in their first appearance variations should be indefinite, indeterminate, and should trend in all directions.

3. Internal-external initiation and causation (tetrakinesis): According to this theory evolution is neither chiefly external (environmental, ontogenetic) nor internal (germinal) but is due to the combined action of internal and external causes accumulated by natural selection. This theory (Osborn), which is based upon the data of paleontology, experimental zoology, and physiology, contains certain elements of both the Lamarckian and the Darwinian interpretations, although it is unlike either. This may be referred to as the principle of the inseparable action of four factors in development (Osborn, 1908.308), as the theory of tetrakinesis in evolution, or as the theory of the action, reaction, and interaction of four complexes of energy under the continuous operation of natural selection (Osborn, 1917.463).

Evidence: According to this interpretation variation should move chiefly along definite lines; it should be orthogenetic; but, unlike the procedure hypothesized by Lamarckian interpretation, variations may or may not be preceded by similar bodily modifications.

ANALYSIS OF THE EVIDENCE ON THE MODES OF ORIGIN OF VARIATION AS CONSIDERED IN DARWINISM, LAMARCKISM, AND TETRAKINESIS

It is obvious that sharp, clear, unbiased observation and analysis of the modes of origin of variations may have a crucial bearing on the choice between the three theories stated above, of the causes of evolution. For example:

1. If in their germinal variations—rectigradations and allometrons—mammals are observed invariably to follow antecedent bodily (somatic) and environmental modifications, such modes of origin would constitute strong evidence for the Lamarckian theory. It will be pointed out, however, that germinal variations do not follow antecedent bodily modifications (somations) as a rule but only in certain instances. These exceptions cast strong doubt on the pure Lamarckian interpretation.

2. If new biocharacters (rectigradations) are heralded in indefinite, indeterminate, accidental variations, by the rudiments of new, spontaneously appearing characters at various points in the teeth and skeleton, if from these unstable origins stability and adaptation are gradually attained by the survival of certain characters and the elimination of others, such modes of origin would constitute strong presumptive evidence in favor of the Darwinian interpretation—namely, that the adaptive arises by selection out of fortuitous variations. If, on the contrary, minor organs, saltations, fluctuations, sports, are observed to have no relation to the main trend of adaptation, this would tend to show that the Darwinian hypothesis affords an inadequate explanation of the evolution of the titanothere.

3. If the modes of variation we have been observing in the titanotheres—rectigradations and allometrons—are in the main definite, determinate, and generally adaptive in direction but do not invariably follow the direction of individual somatic modifications, there must be some cause or complex of causes other than those afforded exclusively by either the pure Lamarckian or the pure Darwinian hypothesis. These rectigradations and allometrons are the modes of variation, observed in the titanotheres and other mammals, which have led Osborn to propose and to develop the theory originally termed (Osborn, 1908. 308) "the four inseparable factors of evolution," more recently termed "the theory of tetrakinesis" (Osborn, 1917.462).

OBSERVED PRINCIPLE OF TETRAPLASTIC DEVELOPMENT OF BODY FORM; THEORETIC PRINCIPLE OF THE TETRAKINETIC EVOLUTION OF THE GERM

Basis of the tetrakinetic theory.—The tetrakinetic theory, which has been developed gradually by the author between the years 1893 and 1917,[62] is based upon the modern conception that the visible bodily evolution of the titanotheres is the result of the invisible germinal evolution of the titanotheres; consequently that the modes of bodily evolution reflect the modes of germinal evolution. If the modes of bodily evolution are orderly, determinate, generally adaptive in direction (entirely distinct from the trial and error modes of pure Darwinism), there must be causes of this orderly evolution of the germ. The conclusion is reached that these causes are not purely internal, germinal, nor purely external, environmental, somatic; that they are in some manner internal-external.

The fourfold principle of development.—It is observed that in the development of its bodily form and function each titanothere is tetraplastic in the sense that from the stage of the fertilized germ to adult age it is plastically molded by the action, reaction, and interaction of four centers of influence, namely, that contained in the heredity germ, that found in the developing organism, that of the life environment,

[62] The special papers and researches in which this principle and theory are treated are listed in the bibliography at the end of this chapter.

and that of the physical environment. If these four influences are all normal (typical) we shall have a typical (normal) titanothere; but if any of these influences is disturbed or altered we shall have an atypical (abnormal) titanothere. Therefore the true interpretation of every titanothere, composed, as it is, of hundreds or thousands of biocharacters, is that each biocharacter is subject to the normal or abnormal condition of these four factors of development. This is the principle that was erroneously termed by the author "the four inseparable factors of evolution." The use of the term "evolution" was an error; the principle should be termed "the four inseparable factors of somatic development," or the principle of tetraplasy.

The theory of the fourfold principle of evolution.—The relation of this principle of tetraplasy in development to the subsequently formulated theory of tetrakinesis in evolution is as follows: The theory of tetrakinesis applies to germinal evolution as distinguished from somatic development; it is based upon the premise that unless the causes of germinal evolution are wholly internal and inherent in the germ itself, a supposition which is not supported by the modes of evolution actually observed, they must be internal-external; they must consist of some kind or degree of physico-chemical (that is, energetic) action, reaction, and interaction between environmental, somatic, and germinal changes which remain to be discovered. Moreover, as all physiological and functional relations thus far observed in mammals are either physical or chemical, and as all physico-chemical relations represent phenomena of energy, we are impelled to believe that the relations between the physical environment, the life environment, the developing organism, and the germ will prove to be "energetic." Hence our theory is termed tetrakinetic (τετρά, four; κινητής, energy) and may be expressed as follows:

In each titanothere the phenomena of life represent the action, reaction, and interaction of four complexes of physico-chemical energy, those of (1) the geographic environment; (2) the developing organism (protoplasm, germ chromatin, of the body cells); (3) the germ chromatin of the reproductive cells, seat of heredity; (4) the life environment. Upon the resultant actions, reactions, and interactions of latent potential (stored) and kinetic (active) energy in each organism natural selection is constantly operating wherever there is competition with the corresponding actions, reactions, and interactions of other titanotheres and other organisms.

According to this energy conception of evolution Darwin's principle of natural selection is not set aside but remains extremely important; it is constantly operating not only between organisms as a whole but on their separate parts, and especially upon their separate manifestations of energy, that have or lack survival value, as shown in the following summary representing the interchange of energy in the developing titanothere and between it and rival or competing titanotheres and other animals. In each animal all the individual changes noted in paragraphs 2, 3, and 4 take place in competition with similar changes in its rivals, under Darwin's law of natural selection.

Diagrammatic exposition of the development of organisms under the tetrakinetic theory

Organism A (the developing titanothere) affected by the actions, reactions, and interactions of		Organisms B–Z (rival or competing titanotheres and other animals) affected by the actions, reactions, and interactions of
1. Physical environment: Physico-chemical energies of space, of the sun, earth, air, and water.		1. Physical environment: Physico-chemical energies of space, of the sun, earth, air, and water.
2. Titanothere organism: Physico-chemical energies of the developing individual in the tissues, cells, protoplasm, and cell chromatin of all biocharacters.	A and B–Z mutually affected through the operation of	2. Animal organisms: Physico-chemical energies of the developing individual in the tissues, cells, protoplasm, and cell chromatin of all biocharacters.
3. Titanothere heredity germ: Physico-chemical energies of the heredity chromatin, included in the reproductive cells and tissues, the predispositions of all biocharacters.	Darwin's law of natural selection, survival of the fittest: competition, and the selection or elimination of energies and forms having or lacking survival value.	3. Animal heredity germ: Physico-chemical energies of the heredity chromatin, included in the reproductive cells and tissues, the predispositions of all biocharacters.
4. Life environment: Physico-chemical energies of other organisms.		4. Life environment: Physico-chemical energies of other organisms.

In explanation of the above summary it may be said that in development the principle of tetraplasy is well established; it rests upon a great variety of observations on the physiology and anatomy—the function and form—of many kinds of plants and animals. According to this principle every biocharacter derives from the germ the potential impulse or energy to reproduce its typical ancestral form or function in the most minute detail. Each biocharacter is tetraplastic (τετρά, four; πλάσσω, to mold) in the sense that its form is molded by the four influences of the germ, the individual development (ontogeny), the physical environment, and the life environment. These influences are complexes of energy and matter

which constantly keep in touch with one another through physico-chemical action, reaction, and interaction. An atypical or abnormal condition, such as excess, depletion, or defect in any one of these four complexes of energy, produces disturbances of some

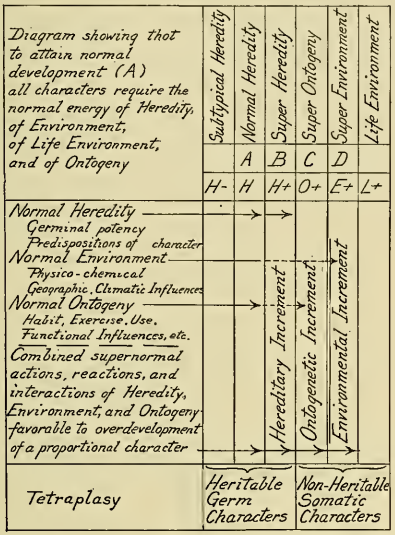


FIGURE 749.—Cumulative or favorable influence of heredity, ontogeny, and environment

kind, and the visible biocharacter ceases to be typical or normal. If such disturbances of normality affect many phases in the development of the biocharacter, the visible organism will be extremely abnormal. Thus to abnormal conditions in the germ, in the ontogeny, in the physical environment, or in the life environment, or in all combined, are attributable the visible abnormalities of the biocharacter. Each of the fourfold influences may convey its separate or its combined effect upon abnormality. It is equally true that departures from the typical condition which may coincide with the adaptive direction of the evolution of the biocharacter may again be fourfold—that is, they may be attributable to favorable predispositions in the germ, favorable modifications and accommodations of the soma, favorable influences of the environment in the form of physico-chemical influence, favorable influences of the life environment in the form of food or of competition, which may favor the development of certain biocharacters, as, for example, the so-called habitudinal (Gulick) and organic (Osborn, 1897.125) selection.

As regards evidence, the theory of tetrakinesis in evolution is quite distinct from the principle of tetraplasy in development. It is in the nature of a trial hypothesis as to the causes of evolution, because we do not yet understand the influence, respectively, of ontogeny, environment, life environment, and selection upon the evolution of the germ. Therefore the theory of tetrakinesis awaits further observation and experiment as to the respective influence of physico-chemical actions, reactions, and interactions on specific biocharacters of the germ.

The following formulae, suggested by Gregory (Osborn, 1912.378, p. 307), present clearly the manner in which we may analyze the possible causes of increment—for example, quantity, intensity, plus and minus variations—in any visible biocharacter wherever we observe and compare members of a series.

QUANTITATIVE INCREMENT OF THE FOUR SEPARABLE FACTORS IN DEVELOPMENT AND EVOLUTION

Let T represent the typical or normal condition of a given biocharacter in the ancestral species as to recti-

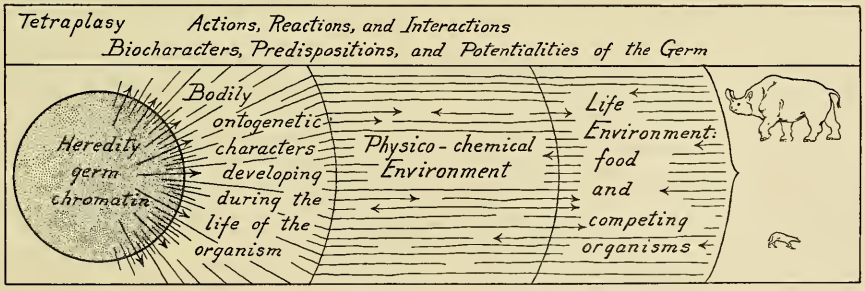


FIGURE 750.—Diagram illustrating the tetraplastic theory

Conception of a centrifugal [→] stream of potential genes, determiners, predispositions, heritages, as passing into the life of the organism from the heredity germ, both into the new reproductive organs and into every cell of the body (chromatin), and as acting, reacting, and interacting with the inorganic environment, the life environment, and the ontogeny of the organism itself. At present there is comparatively little direct evidence of a centripetal [←] or reversed current of energy such as to effect specific changes in the heredity chromatin.

gradation, allometry, area, volume, degree, or intensity of coloring, strength of muscle, or any biocharacter capable of quantitative determination. Let T_n

represent the average condition of the same biocharacter in a species or mutation descendant from T. Then $T_n - T$ is the measure of the evolution of the biocharacter, and 100 $(T_n - T)$ T is its percentage increment. Hence

$$T_n = T + \left(\frac{P}{100}\right)T$$

where $\frac{P}{100}$ represents the total percentage increment.

Suppose that this total percentage of increment in the biocharacter were made up of the following contributory increments:

H (heredity), that part of the total percentage increment which may be ascribed hypothetically to an orthogenetic or germinal tendency to accelerate, balance, or retard the typical condition of T.

O (ontogeny), that part of the total percentage increment which may be ascribed hypothetically to modifications arising in the soma, evoked either by use and disuse or by physico-chemical correlation (interaction) during individual development.

E (environment), that part of the total percentage increment which may be ascribed hypothetically to the reaction to the geographic and physical environment.

L.E (life environment), that part of the total percentage increment which may be ascribed hypothetically to the action of surrounding titanotheres and other organisms.

S (selection), that part of the total percentage increment which may be ascribed to the cumulative effect of natural selection upon germinal variations, fluctuations, etc.

Substituting the above symbols in the formula

$$T_n = T + \left(\frac{P}{100}\right)T$$

we obtain the formula

$$T_n = T + \left(\frac{H+O+E+L.E+S}{100}\right)T$$

whence

$$H+O+E+L.E = 100 + S\left(\frac{T_n - T}{T}\right)$$

In paleontologic research on certain proportion biocharacters in continuous phyla one may be able to determine the numerical value of $T_n - \frac{T}{T}$, and hence to obtain an exact measure of the total percentage of increment due to the combined action of H+O+E+L.E+S taken together, but not to measure any one of these factors separately.

In the application of the tetrakinetic theory it is the causes of the invisible, germinal increment which we have to explain—the increment, for example, which separates the germ of *Brontotherium* from that of *Eotitanops*.

It is not claimed that the theory of tetrakinesis, in which the incessant action of natural selection plays a large part, will explain the origin of a single biocharacter, rectigradation, or allometron. It is still in the stage of a working hypothesis, to be tested by observation and experiment, in the way, for example, that the original Lamarckian and Darwinian theories have been and are being tested. The only insight we now have into the possible working of this theory is afforded by the phenomena of organic selection and of interaction in the changes in the velocity of certain biocharacters which are known to be due in the soma to the circulation in the system of "physico-chemical messengers" of the kind designated among physiologists as enzymes and internal secretions, including the hormones (accelerators) and chalones (retarders) of the individual growth of certain biocharacters. So far as known at present these are purely somatic phenomena. Experiment may prove that similar interactions originally arising through adaptive modifications of the body (soma) may affect the corresponding predispositions and potentialities of the germ.

FIGURE 751.—Diagram illustrating the principle of tetraplasy

Representing the conception of a centrifugal stream of potential heritages and predispositions passing from the heredity germ into the life of the organism (ontogeny), both into the new reproductive organs and into every cell of the body (protoplasm and cell chromatin), as acting, reacting, and interacting with all the other functions and structures within the body as well as with the stream of energy interchanged between the body and the physical environment and the life environment, showing that every visible biocharacter represents the action, reaction, and interaction of these four complexes of energy.

ANALYSIS OF THE MODES OF VARIATION; THEORETIC IMPORTANCE OF INITIATION

We have set forth above an analysis of the modes of variation; let us apply this analysis to proportions.

Until the causes, as yet unknown, of predisposition, of increment, of acceleration, of retardation, of rectigradation, of allometry in the germ itself are discovered experimentally we must confine our observations to what we see going on in the body and must seek to answer the all-important question whether the initia-

tion of any given biocharacter is environmental, somatic, or germinal. If, for example, in all the instances observed the inititation of a certain allometron is primarily somatic and secondarily germinal, this fact would be presumptive evidence that in this particular biocharacter somatic action, reaction, and interaction precede germinal predisposition. Even if it were proved that a certain allometron is invariably somatic in its initiation and secondarily germinal, it would not be logical to assume that all allometry is first somatic and then germinal; in fact, we shall point out that certain allometrons are germinal from the first; they are not, so far as we know, initiated in ontogeny. Moreover, invariable sequence is not invariable cause and effect.

BEARING OF SALTATION VERSUS CONTINUITY ON THE LAMARCKIAN, DARWINIAN, AND TETRAKINETIC THEORIES

According to the Darwinian theory variations should be observed as chiefly discontinuous, saltatory, fortuitous, adaptive or nonadaptive, furnishing material for natural selection.

According to the Lamarckian and the tetrakinetic theories variations should be mainly continuous and adaptive, rarely saltatory and fortuitous. What are the observed facts of variation?

DARWIN'S HYPOTHESIS OF FORTUITOUS SALTATION AND FLUCTUATION

After years of observation of domesticated plants and animals under artificial selection, Darwin reached the conclusion that there were three kinds of new variation characters for natural selection to work upon—first, hereditary minor saltations ("minute heritable variations"); second, hereditary fluctuations of proportion; third, somatogenic modifications of proportion, which he finally believed (Lamarckian theory) to be inherited.

Darwin (1859.1) held that evolution is due chiefly to the natural selection of "heritable individual differences"—that is, variations—his real meaning as to these individual differences being found in the hundreds of examples he cited in the "Origin of species" and in "Variations of animals and plants under domestication." Poulton (1909.1, pp. 49–50) remarks as to Darwin: "His observation and study of nature led him to the conviction that large variations [that is, major saltations], although abundant, were rarely selected, but that evolution proceeded gradually and by small steps." Plate (1909.1) established clearly that the "individual differences" of Darwin are practically identical with the "mutations" of De Vries. Osborn (1912.362, pp. 76–82) held that Darwin's conception was that evolution develops chiefly through the natural selection of minor saltations; but that Darwin's "individual differences" are in the nature of both major and minor saltations, structural or functional, and always hereditary, as is shown in the observations that he assembled in commenting on the genesis of the race horse and of the greyhound, breeds which he used by way of illustration of the genesis of new forms in nature. In considering these breeds he pointed to such suddenly appearing new characters as horn rudiments, tail-lessness, curliness of the hair, characters which are "discontinuous" in Bateson's sense, "mutations" in that of De Vries. Intermingled with these minor saltations Darwin cited others which are obviously reversional. That he believed chiefly in the accumulation of favorable minor saltations there can be no question, but, for the admirable reason that no evidence had been adduced in nature of evolution by major saltations, he rejected the hypothesis, which originated with Geoffroy St. Hilaire, of the appearance under certain environmental conditions of entirely new types of animals and plants or of new profoundly modified organs.

In brief, Darwin held chiefly that by cumulative natural selection of minor saltations a character could slowly be shifted in an adaptive direction. These minor saltations were in his opinion the fortuitous or chance material out of which nature "selects" its adaptations, utilizing the adaptive and rejecting the inadaptive. He guarded the word "chance," however, by stating that it might merely cover our ignorance of the unknown causes of variation.

Darwin also believed in the natural selection of heritable fluctuations of proportion, as illustrated in his classic rebuttal of the Lamarckian explanation of the mode of origin of the long neck of the giraffe, namely:

> So under nature with the nascent giraffe, the individuals which were the highest browsers and were able during dearths to reach even an inch or two above the others will often have been preserved; for they will have roamed over the whole country in search of food. * * * These slight proportional differences will favor survival and will be transmitted to offspring. ("Origin of species," ed. of Appleton, 1909, p. 27.)

Naturally Darwin could not draw such sharp distinctions in the definition of variation either in language or in example as we may to-day, profiting as we do by the 50 years of experiment and analysis that have passed since his time. The chief emphasis in the above passage is in the words "slight proportional differences," differences that we now classify as fluctuations or fluctuating variabilities.

In conclusion, critical reexamination of Darwin's writings leads us to dissent entirely from the influential opinion of De Vries that there was always a doubt in Darwin's mind as to whether (1) the selection of minor saltations or (2) the selection of fluctuations played the larger part in the origin of species. The actual examples that Darwin cited and his repeated emphasis prove that minor saltations like the De

Vries mutations were chiefly in his mind. This raises the inquiry as to the normal or abnormal character of major and minor saltations.

MOST SALTATIONS IN MAMMALS ABNORMAL

Are saltations natural or artificial products? Are they normal or abnormal? Against the repeatedly observed continuous origin of normal adaptive rectigradations and allometrons in titanotheres and other quadrupeds still stands the pure Darwinian hypothesis of the fortuitous and discontinuous origin of similar biocharacters as material for natural selection.

It is true that some characters, such as horns, do arise suddenly. It is therefore interesting to compare 20 distinct types or kinds of major and minor saltations in 11 different families of mammals—man, horses, cattle, sheep, deer, pigs, dogs, cats, rabbits, guinea pigs, mice, in which saltations that are closely or exactly similar repeatedly occur. Our chief authorities are Allen, Azara, Bateson, Brinkerhoff, Castle, Darwin, Davenport, Haeckel, Percival, Poulton, Ridgeway, Root, Seton, Sutton, Twining. The accompanying table presents the very impressive results obtained by this comparison.

Comparison of twenty saltations in eleven kinds of mammals

	Man	Horses	Cattle	Sheep	Deer	Pigs	Dogs	Cats	Rabbits	Guinea pigs	Mice
Neoproportions (allometrons):											
1. Brachyopy (abbreviation of the face)			×				×				
2. Brachymely (short-leggedness)			×	×			×				
Horn saltations, horn biocharacters:											
3. Sudden development of horns in hornless races	×	×							×		
4. Sudden disappearance of horns in horned races			×	×							
5. Supernumerary horns in horned races				×							
6. Transverse duplication of horns				×							
7. Absence of one horn in horned races					×						
Loss of biocharacters:											
8. Earlessness (absence of both external ears)											
9. Loss of one of the external ears									×		
10. Taillessness (absence of caudal vertebrae)	×	×		×				×		×	
11. Hairlessness (entire absence of hair)		×	×				×				×
Saltations of form:											
12. Excessively fine or silky hair	×		×	×				×	×		×
13. Reversed hair patches			×							×	
14. Curled hair over the entire body	×	×		×			×				
15. Excessive hairiness or length of hair	×	×	×	×			×	×	×	×	
16. Local or general epidermal thickenings	×										×
17. Mottled skin markings	×	×	×			×					
Foot biocharacters:											
18. Polydactylism (supernumerary digits)	×	×	×	×	×	×	×	×		×	
19. Syndactylism (consolidation of paired hoofs)			×			×					
Jaw biocharacters:											
20. Supernumerary jaw appendages	×			×		×					

Teratology and Mendelism have alike revealed the fact that most saltations represent failures or abnormalities in the germinal mechanism. Some occur under natural conditions, but most of them under artificial conditions of environment. Many of these saltations are dominant characters in heredity, and in some domestic breeds, through either artificial selection or failure of artificial selection, they become fairly numerous. We have tailless cats, solid-footed (syndactyl) pigs, polydactyl cats, curly-haired horses, short-legged sheep (ancon), and hornless cattle of several breeds (Angus, niata). It is possible also that races of wild animals have been established through germinal saltations, such as the four-horned antelope of India (*Tetracerus*), which is comparable to the four-horned domestic breed of sheep.

Paleontologic and anatomical research on the mammals for over a century has failed to demonstrate in a state of nature a single example of the sudden origin of such important characters as the horns. There is reason to believe that if peculiar or anomalous mammals do arise under natural conditions they are driven away from the herds and not allowed to breed. Thus it may be said that in neither zoology nor paleontology has any evidence been adduced thus far of the saltatory origin of allometrons or rectigradations under natural conditions.

Bateson (1894.1) revived the saltation hypothesis of Darwin as the exclusive mode of the origin of species. Saltationists, now known as mutationists (of De Vries), refer to Bateson's work as laying the sure foundations for the theory of the origin of species through heritable saltations. At the time Bateson's work appeared it suffered a searching review from Scott (1894.1, pp. 355–374). Matthew (Osborn, 1912.372) examined it critically in the light of vertebrate paleontology and reached the following conclusions:

> Of the 323 cases of discontinuity cited in mammals the greater part are obviously teratological and have no direct significance in relation to paleontologic evolution except for a very few instances such as the supernumerary or fourth molar teeth of *Otocyon*. While not significant [in evolution] these teratological cases are interesting because they show the prevalence of homoeosis and indicate that many of the remaining cases which might [otherwise] be considered normal saltations or reversions may actually be teratologic, but disguised by homoeosis; all of the possibly significant cases (such as the supernumerary molars) are thereby placed under suspicion. Setting aside this suspicion the minority of the "significant" cases in teeth and feet may be said to afford evidence of the meristic variability of vestigial and rudimentary structures. Bateson's statement that such variability is related not to nonfunctionalism but to terminal position in a series appears to me directly in conflict with his [Bateson's] own evidence, as it certainly is with all my experience. This accords with commonly observed data in paleontology, for no paleontologist would question that vestigial teeth or bones are apt to [finally] disappear by "discontinuous" evolution. As to the appearance by salatory evolution of new and primarily functional parts in teeth or feet, I know of no adequate paleontologic evidence in its favor. It is either demonstrably false or decidedly improbable. In the cases of supernumerary teeth (*Otocyon*, *Myrmecobius*, Cetacea, etc.) saltatory evolution may be regarded as reasonable in default of any paleontologic evidence to the contrary. Meristic or numerical evolution in fully functional vertebrae is intrinsically probable as the only method of evolutionary change.
>
> The fact that so many cases of supernumerary teeth are associated with asymmetry throws doubt on the significance of all such cases; asymmetric variations and those occurring only in upper or only in lower teeth have no analogy in paleontology; such cases as occur abnormally are recognized as of a different and nonsignificant class than normal evolutionary changes.

Summary of Bateson's 323 cases

	Nonsignificant	Possibly significant	Variations vestigial or reversional
1. Vertebrae	17	27	
2. Teeth	83	10	76
3. Feet	110		
	210	37	76

The summary of our conclusions is as follows:

Of the 323 cases cited by Bateson of discontinuity in the vertebrae, the teeth, and the skulls of modern mammals, 286 are abnormal, teratological, reversional, and have absolutely no significance in evolution. Ten cases of additional fourth molar teeth are possibly of significance, because among the mammals there are a few genera with fourth molars, which probably have arisen by saltation, as in *Otocyon* and certain African races of *Homo*. Of all the cases cited by Bateson there remain only 27 which may be ranked as probably significant—that is, of the kind which may be of actual importance in normal evolution. These are the addition or the reduction of the number of vertebrae in the spinal column, which is of real significance because of the well-known variations in the vertebral formulae observed among the different genera and even species of mammals, such as *Equus caballus* (Nordic breed), with six lumbar vertebrae, and *E. caballus* (Arab breed), with five lumbar vertebrae. The occasional "origin of species" through vertebral saltation is also rendered probable by the fact that vertebrae can be added to or subtracted from the spinal column only discontinuously—that is, through germinal saltation.

This evidence, in its bearing on the principle that conspicuous major saltations are not a part of the normal evolution of mammals, also throws prima facie doubt upon the less conspicuous, minor saltations. It is these saltations which, as stated above, Darwin believed to be among the chief materials out of which adaptations were accumulated through the action of natural selection. The only known difference between major and minor saltations is one of degree, not of kind.

The fact that the vast majority of germinal anomalies cited in Bateson's researches have no significance in evolution under natural conditions, with the exception of the sudden addition or disappearance of completely adaptive organs, like vertebrae and teeth, also throws many minor germinal saltations under suspicion as material for natural selection, important as they doubtless are in artificial selection and hybridization. This opinion may be contrasted with that of Punnett (1911.1, p. 15):

> Speaking generally, species do not grade gradually from one to the other, but the differences between them are sharp and specific. Whence comes this prevalence of discontinuity if the process by which they have arisen is one of accumulation of minute and almost imperceptible differences? Why are not intermediates of all sorts more abundantly produced in nature than is actually known to be the case?

The fact is that intermediates are found abundantly in mammalian zoology (see, for example, Osgood, 1909.1) as well as in paleontology.

MENDELIAN DISCONTINUITY IN HEREDITY

In 1903 the saltation hypothesis was again revived, after the rediscovery of the law of Mendel (1865). The wide prevalence of the separable characters in heredity and of the separateness of so-called "unit char-

acters" as they appear in the body, and the demonstrated separableness of their "factors," "determiners," "genes" in the germ, gave rise afresh to the theoretic assumption of discontinuity of origin of all characters in the germ. In 1912 (1912.372) Osborn established the fact that this assumption is a non sequitur.

Mendelian research on the mammals has been confined mainly to color characters in certain species of rodents, chiefly mice and guinea pigs, although it has been extended also to horses and cattle, which were studied less by experiment than from the records of stud books. The first striking general result is the principle of antithesis in the heritage of characters that mutually exclude each other, as originally typified by the antithesis of Mendel's "tallness" and "shortness," "smooth coat" and "wrinkled coat" in peas. The second Mendelian principle is that when these antithetic characters meet in the germ cells the dominant character becomes visible or patent in the offspring, whereas the recessive character remains latent in the germ, perhaps to reappear in later crosses in the Mendelian ratios.

Similar dominance of head proportion appears in the first cross between the ass (♂) and horse (♀) as exemplified in the mule, which exhibits the dominant dolichocephaly of the horse and at the same time the dominant molar-tooth pattern of the ass. Other proportional characters in this hybrid are known to be imperfectly "dominant," or "blending." In such cases inheritance is blending and non-Mendelian, for there is no evidence of size character segregation in the germ other than the increased variability of the second hybrid generation.

TRUTH AND ERROR IN JOHANNSEN'S PURE LINE SALTATION PRINCIPLE

The "pure line" is another biologic principle from which both true and false conclusions have been drawn. This principle is based upon breeding experiments on pure strains of garden beans which tend to show that certain kinds of characters arise only discontinuously by saltation. Johannsen (1911.1, pp. 129–159), through experiments on successive generations of self-fertilizing plants (the garden bean), reached the illogical opinion as to all plants and animals that the apparent continuity of visible, somatic form is delusive, and that in the origin of "mutations" and "species" there is invariably a germinal saltation or discontinuity. His opinions may be summarized and paraphrased as follows:

> The developing organism which the paleontologist or the zoologist observes may be called the phenotype, or visible type. Vertebrate paleontologists and zoologists comparing huge collections in museums have erected in phylogenetic speculation a science of phenotypes which is not of value in a study of germinal evolution (genetics) because the description of phenotypes is inadequate as the starting point for genetic investigation. The adaptation of phenotypes through the direct influence of environment [Buffon's factor] or of use and disuse [Lamarck's factor] is not of genetic [hereditary] importance. Ontogeny is an expression of the heredity germ, but the heredity germ is not affected by ontogenesis. The conception of evolution by continuous transitions from one type to another has imposed itself upon zoologists, botanists [and paleontologists] who are examining chiefly shifting visible forms in very fine gradations. There may be such a continuity in visible form but not in the heredity germ from which they spring. All degrees of continuity between phenotypes may be found, but real germinal transitions must be distinguished from the transitions which we observe in visible museum specimens.
>
> The delusive nature of phenotype continuity is shown by the examination of pure lines of plants. A typical pure line is composed of the descendants of one pure strain of an organism exclusively propagated by self-fertilization, as in the case of the garden bean, which demonstrates the stability of germinal constitution in successive generations where undisturbed by cross breeding with other strains.
>
> Johannsen proposes the term gene to designate the germinal "factors," "determiners" (of authors), of various visible characters. The sum total of all the genes in the fertilized germ cell he terms the genotype. A group of similar genotypes—that is, of pure-strain individuals—he terms the biotype. The genotype, the sum total of the genes, can be examined only by the qualities and reactions of the phenotypes under experiment. Such examination shows that within pure lines—if no mutations (De Vries) or other disturbances have been at work—there are no genotypical (that is, germinal) differences in the characters under examination. For example, the mutations of De Vries observed in nature have shown themselves as considerable discontinuous saltations.

The fallacy of Johannsen's argument lies in the dictum "ab uno disce omnes." He may be entirely right as to the origin of certain germinal characters and entirely wrong as to the origin of others. Nevertheless, he concludes from his observations on the bean that the essential point in all evolution is the sudden alteration, loss or gain, of the genes, the germinal constituents, of the genotype. In his opinion all evidence as to "mutations of De Vries" points to the discontinuity of the changes in question. In the theory of origin of allometrons, the crucial point in the application of Johannsen's pure-line hypothesis would be the assumed stability of the genes, factors, or determiners, as distinguished from their assumed fluctuation.

EXPERIMENTS IN THE ARTIFICIAL SELECTION OF VARIATIONS OF PROPORTION

Against such hypotheses of the stability of all germinal determiners of proportional, quantitative, intensive characters may be set the evidence adduced by many experimentalists as to the heritage of quantitative variation. As opposed to Johannsen, Castle (1916.1) observes that in his experiments every "unit character"—that is, every germinal determiner—is subject to quantitative variation—that is, its visible expression in the body varies—and it is clear that these variations have a germinal basis, because they are inherited. By selection, plus or minus, through a series of generations we can intensify

or diminish the expression of a character—that is, we can modify the germinal character itself. These germinal quantitative variations (in color patterns and pigmented areas) behave as simple units—that is, biocharacters. Blending of size (Castle, 1916.1) is demonstrated in rabbits, in which the offspring of a large and a small rabbit are of intermediate size—that is, neither small size nor large size dominating in the cross. "Size," observes Castle, "is an unstable character, ever varying." Slow changes in size can be effected by artificial selection without any crossing whatever. Progressive diminution in size may be effected by crossing small breeds.

More recently Jennings (1917.1, p. 305) observes:

> It appears to me that the experimental work in Mendelism * * * is supplying a complete foundation for evolution through the accumulation by [artificial] selection of minute gradation. * * * A visible character may be modified in the finest gradations by alterations in diverse parts of the germinal material. The objections raised by the mutationists to gradual change through [artificial] selection are breaking down as a result of the thoroughness of the mutationists' own studies.

Jennings is of the opinion (op. cit., p. 306) that Mendelian heredity acts as an accelerator to the effectiveness of [artificial] selection. The sum of Castle's and Jennings's observations and opinions is that certain germinal characters may be altered by artificially selecting in each generation the merely quantitative variation that goes farthest in the desired direction.

Against this general experimental conclusion are earlier (Punnett, 1911.1, p. 138; Davenport, 1910) and more recent (Pearl, 1917.1, pp. 72, 73) observations that in certain biocharacters fluctuations are not heritable, and that it is impossible through cumulative artificial selection of fluctuations to establish a new quantitative mean.

To sum up: The years of experiment since the rediscovery of Mendelism in 1903 present considerable but not yet conclusive evidence that certain proportional characters as well as certain numerically new characters can be accumulated through artificial selection, and that certain other characters are not cumulative through artificial selection of quantitative variations but are dependent upon the saltation, or sudden appearance, of new character genes or sudden gradations of character in the germ.

The observations (Castle, Jennings) in experimental heredity that certain germinal quantitative variations of form and color are heritable and can be guided in certain directions by artificial selection do not necessarily prove that allometrons have arisen by similar processes under natural selection but render it probable that heritable fluctuations of proportion of survival value are selected and accumulated under natural selection, as in Darwin's theory of the causes of the long neck of the giraffe.

THEORETIC AND EXPERIMENTAL CAUSES OF THE EVOLUTION OF ALLOMETRONS

The above studies in experimental heredity and selection have a very important bearing upon our interpretations of heredity in the titanotheres and other quadrupeds known from their fossilized remains. It should not be assumed that all allometrons are due to the same causes.

Among titanotheres adaptation through changes of proportion has been shown to constitute the larger part of the bodily evolution. In all mammals the response of the musculature and the skeleton to changes of environment and habitat is more conspicuous in proportions than in any other character groups. Allometric adaptation includes a continuous and perfect adjustment of all the demands of weight and speed in locomotion and of offense and defense in the capture or warding off of enemies. It follows, as already remarked, that evidence for the Lamarckian, the Darwinian, and the tetrakinetic theories of causation must be most closely analyzed. The following 12 modes of allometric change, germinal, ontogenetic, environmental, selectional, are observable:

1. Germinal allometrons, arising by continuous or gradual change.
2. Germinal allometrons, arising by sudden changes (saltations).
3. Certain germinal allometrons, uninfluenced by the direct action of environment.
4. Germinal allometrons, apparently influenced by direct action of environment.
5. Germinal allometrons, fluctuating and nonfluctuating.
6. Certain germinal allometrons, of high survival selection value.
7. Other germinal allometrons, of apparently no survival selection value.
8. Ontogenetic allometrons, experimentally influenced by changes of habit.
9. Ontogenetic allometrons, experimentally influenced by changes of environment.
10. Germinal allometrons—prenatal, adolescent, adult, male sexual, and female sexual development.
11. Ontogenic allometrons, influenced by glandular internal secretions, enzymes, and other organic catalyzers.
12. Germinal (?) allometrons, influenced by organic catalyzers.

GERMINAL ALLOMETRONS ARISING BY CONTINUOUS OR GRADUAL CHANGE

The continuity of proportional change observed in all the phyla of titanotheres described in this monograph, as well as in several other phyla of ungulates, such as the rhinoceroses and the horses, constitutes in itself very strong evidence against the adequacy of the Darwinian theory of the natural selection of individual fluctuations.

Proportional contiuuity is in the nature of the continuous "mutations of Waagen" rather than of the discontinuous "mutations of De Vries." The general contrast is very ably presented by Scott (1894.7, p. 355) in his article entitled "Mutations and variations." Progressive brachycephaly and progressive dolichocephaly in the titanotheres point to the presence of

some similarly acting influence affecting generation after generation in a similar manner, operating like the "Mutationsrichtung" of Neumayr. Within certain phyla a tendency or predetermination to evolve in breadth or length orthogenetically appears to be established, flowing in one direction like a tide, on the surface of which occur individual fluctuations and variations, like waves and ripples. The overdevelopment of certain proportions, as seen in extreme brachycephaly and dolichocephaly, for example, seems to be a manifestation of this orthogenetic impulse, which appears to carry certain skulls to inadaptive extremes. As shown in section 2 of this chapter, on the causes of extinction, such extremes of structure tend to be eliminated in the struggle for existence and to be replaced by head forms of intermediate development.

The phenomenon of overevolution has been likened by Loomis to the principle of "momentum" in mechanics. As described below it appears as if certain progressive proportions were continually influenced by certain internal secretions, or organic catalyzers, which continue to accelerate these allometric biocharacters in generation after generation and finally to overaccelerate them beyond the point of utility. This is manifest in certain cases of the harmonic, uniform dolichocephaly or brachycephaly of the greater part of the skull, where certain parts are sacrificed or overcrowded, in apparent defiance of the principle of compensation. Again, as macrocephaly and microcephaly arise as abnormalities due to abnormal internal secretions, it would appear probable that normal internal secretions are in some way connected with the normal evolution of head proportions.

Subject to future experimental test it would appear probable that continuity of head form evolution is not caused through the Darwinian principle of continuous selection of "individual variations" and "individual fluctuations" but by the intermediate influence of some kind of interaction, as implied in the tetrakinetic theory.

GERMINAL ALLOMETRONS ARISING BY SUDDEN CHANGES (SALTATIONS); INTERACTION THEORY

In considering major saltations above we have alluded briefly to the numerous examples of the sudden appearance of germinal allometrons in domesticated animals, such as are seen in the short-limbed ancon breed of sheep. No evidence has thus far been adduced that any wild breeds of animals have originated suddenly in this way. The fact that all four limbs in quadrupeds are similarly affected by harmonic abbreviation in cases of sudden brachymely and that the opposite hands in bipeds are similarly affected in cases of sudden brachydactyly points again to the possibility of abnormal chemical messenger interaction as being the immediate cause of these kinds of abbreviation. There are in man two kinds of brachydactyly—(1) that in which the hand is harmonically abbreviated and (2) that in which the terminal phalanges are lacking. The former, congenital brachydactyly, bears strong superficial resemblance to the ontogenetic brachydactyly caused by the abnormal internal secretions of certain parts of the pituitary gland (Cushing, 1912.1). This again suggests the hypothesis that congenital brachymely and brachydactyly are due to congenital defects in the hereditary chemical messenger interaction system. The value of this hypothesis can be tested only by physiological experiment. So far as they are understood these phenomena of discontinuity of proportion, like the phenomena of continuity of proportion, appear to be connected with some internal interacting chemical messenger system, which may be at once the seat of balance, of retardation, and of the sudden acceleration manifested in saltations of proportions.

CERTAIN GERMINAL ALLOMETRONS UNINFLUENCED BY THE DIRECT ACTION OF ENVIRONMENT

Apart from the well-known influence of environment on harmonic size, dwarfing or gigantism, the field, experimental, and anatomical evidence on the influence of environment on germinal allometrons is conflicting. As to field zoologic observations Gerrit S. Miller (letter to author, 1912) observes:

> I can give you plenty of illustrations of "direct action of environment" on color characters in mammals; in fact, you have only to tell me how many you want, and I will fill your order. As to proportions, size, and cranial characters, the case is quite different. So far as I have been able to make out the action is here indirect, as, for instance, when a cat in a wet district takes to a fish diet and [ontogenetically] develops the characters of *Aelurus*, or when a viverrid does the same and becomes *Cynogale*. You can hardly say that the differences here observed are due to the direct action of the environment. They are rather due to the ontogenetic modifications caused by habit. I know of plenty of cases of color changes of definite character affecting many different members of a fauna in the same way, as you go from a wet to a dry region, or from a high to a low region, but I do not know of any parallel set of changes in proportions, size, or structure.

The field zoologist has yet to demonstrate that there is direct relation between certain environments and certain allometrons distinct from the indirect action of environment which may arise as the ontogenic result of differences of locomotion, of food, and of feeding habits in different environments, as, for example, the influence of the purely carnivorous diet of the Eskimo on their head and jaw conformation. The ichthyologists (Jordan, Evermann) demonstrate that the ontogenic proportions of spines in certain fishes are directly related to the chemical content of their watery medium.

Anthropologists differ somewhat as to the direct action of environment on the evolution of the form of the human head. Elliot Smith (letter to author, August 12, 1911) finds no evidence that environment

directly produces any modification of head proportion. He implies that such modification, if natural, would show only after thousands of years of residence in a single locality, during which the indirect influence of change of feeding habits might play an important part. He continues:

> I do not believe for a moment in Boas's observations [of 1911] on the direct and rapid influence of environment in modifying ontogenic head form. In my opinion the conditions of dolichocephaly and brachycephaly in man must have developed very slowly through exceedingly long periods of time and in widely separated areas, amidst widely different environments. Brachycephaly has thus become especially distinctive of the Central Asian high plateau populations, dolichocephaly of the littoral and plains-dwelling peoples. But these unit characters are now so fixed that environment is powerless to modify them in a thousand years or so.

The observations of Hrdlička (1910.1, p. 214) on the forms of the cranial vault and the face of the Eskimo lead us to believe that they are attributable rather to feeding habits than to the direct action of environment.

Apart from the differences of opinion as to the direct influence of environment on head form as distinguished from the modifications of habit and the influence of human selection, there is absolute unanimity both of evidence and of opinion as to the continuity of allometric evolution in the human species which establishes different extremes of head form under conditions of geographic and social isolation.

GERMINAL ALLOMETRONS APPARENTLY INFLUENCED BY DIRECT ACTION OF ENVIRONMENT

The dwarfing as well as the gigantism that arise continuously or suddenly are usually harmonic—that is, all parts are contracted or enlarged harmoniously owing to generally unfavorable or highly favorable environmental conditions. This is generally true of dwarfed breeds that arise through long-continued exposure to a dwarfing environment. For example, the Celtic pony (*E. caballus celticus* Ewart) appears to be a harmonic dwarf of its remote Arab-like ancestor. Doubtless disharmonic dwarfing and gigantism arise under the prolonged direct action of the environment, but at present no examples can be cited.

It would be interesting to ascertain through experiment whether there is any relation between the harmonic dwarfing attributable to a prolonged unfavorable environment on successive generations and that induced experimentally in a few months by removal of the thyroid or parathyroid glands, as observed in dogs and sheep. It does not appear probable that any relation will be found, because thyroid and parathyroid dwarfing is apt to be disharmonic, causing the acceleration of some parts and the general retardation of others.

GERMINAL ALLOMETRONS, FLUCTUATING AND NONFLUCTUATING

The Darwinian theory, as we have shown above, depends upon the continuous natural selection of "fluctuating variations" that are continous in a given direction. It appears to be highly probable as to fluctuations that have high survival selection value, such as fluctuations in the length in the entire series of cervical vertebrae in the neck of the giraffe, an evolution which is generally harmonic. Harmonic allometrons generally, such as length of neck, length of limb, length of feet, may possess high survival selection value and favor the Darwinian theory.

The causation of disharmonic allometrons, which in the titanothere skull are far more numerous than the harmonic, presents, on the contrary, great theoretic difficulties. The abbreviation of the face coordinately with the elongation of the cranium is an example of disharmony. The separate velocity of ontogenetic and phylogenetic movement of a very large number of biocharacters is so perfectly coordinated and adjusted in every stage of development and evolution as to make the Darwinian "fortuitous fluctuation" hypothesis in a high degree untenable.

CERTAIN GERMINAL ALLOMETRONS OF HIGH SURVIVAL SELECTION VALUE

All parts of the skeleton change in proportion during the entire period of growth, prenatal and postnatal. These changes of proportion are partly paleotelic—that is, they are reversive to ancestral stages—partly cenotelic—that is, they are adapted to existing conditions.

Certain prenatal germinal proportions exhibit especially high survival value; they are examples of perfect mechanical adjustments of form that rise from the germ before they have been developed by individual modification. Apparently fatal to the Lamarckian theory that all allometrons are due to the inheritance of modifications acquired postnatally are the many well-known instances of prenatal allometrons, such as those of certain precocious birds—the Praecoces, for example—which are adapted to run immediately on leaving the shell. Certain precocious desert-living cursorial mammals are also capable of rapid movement immediately after birth. The limbs of such animals have before birth the proportions of those of adults. Conspicuous among these are the horses. In the feral state the foals must be able immediately after birth to keep up with the herd, and in adaptation to this necessity the members that contribute most to speed are prenatally so much accelerated in development that they attain almost their full adult length before birth. Thus in thoroughbred horses the postnatal increase in the length of the cannon bones is only 3 centimeters

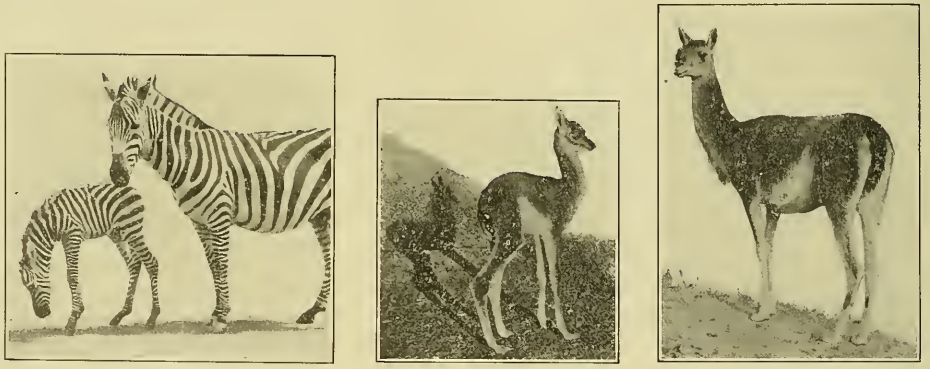
(Ewart, 1909.1). Osborn observed the survival value of these limb proportions among the semiferal mustangs of western Louisiana. While the herd was being rounded up one of the mares began to give birth to a colt; she lay down for a moment, the foal was cast, and in an incredibly short time the mother and foal were running with the herd. Stevenson-Hamilton (1912.1, p. 539) observes that within a few hours after birth all young antelopes and zebras, owing to their limb proportions, are able to keep up in the most surprising manner with the full-grown animals, even when those are going at full speed.

These are instances where the Darwinian theory of the selection of germinal fluctuations of proportion appears to be applicable; whereas the Lamarckian theory of the inheritance of acquired changes of proportion is apparently not applicable. They are notable instances of the high survival value of certain allometrons which are apparently initiated in the germ before they are initiated in ontogeny.

ONTOGENETIC ALLOMETRONS EXPERIMENTALLY INFLUENCED BY CHANGES OF HABIT

The reverse principle is equally true, namely, that certain adaptive proportions are initiated in ontogeny. Notable instances of this principle are found in the experiments of Regnault (1911.1), whereby it is demonstrated that cursorial limb proportions may be transformed into saltatory limb proportions experimentally.

In the normal dog the tibiofemoral proportion—that is, length of the tibia as compared with that of the femur—is 95 per cent. The percentage rises to 104 in dogs that are forced congenitally or experimentally into the cursorial habit. Thus a dog born without fore legs sits upright and learns to progress by imperfect or awkward leaps, in response to which the tibia gradually elongates. Similar results are recorded by Fuld (1901.1) through the amputation of the fore limbs in newborn dogs, in which, through the enforced adoption of the saltatory gait, the tibiofemoral index rises to 101–104 as compared with 95 in the normal dog. At the same time the femur and tibia, taking on the entire weight of the body in locomotion, become more massive and exhibit many marked modifications.



A B¹ B

FIGURE 752.—Accelerated elongation of the limbs in the young zebra and guanaco

A, Zebra and colt; B, guanaco; B¹, young guanaco. Note the relative length of limb which enables the animal at birth to keep up with its mother. Modified after Loomis.

OTHER GERMINAL ALLOMETRONS OF APPARENTLY NO SURVIVAL SELECTION VALUE; PREDETERMINATION

No anthropologist has offered any satisfactory explanation as to the adaptive significance of the dolichocephaly and brachycephaly of the human head. Broad heads and long heads have lived in northern Europe for 30,000 years under the same environment, with the same feeding habits and under the same social conditions, and without displaying marked differences of intellectual aptitudes. As to causation Boas writes (letter to author, April 8, 1911):

> So far, the matter [of the origin and cause of head form] is very perplexing to me. I feel, however, very strongly that changes in type [in head proportion] are very liable to be progressive in definite directions. * * * To my mind it seems no more difficult to assume that this predetermined direction should continue from generation to generation than to make the much more difficult assumption that notwithstanding all internal changes the egg cell of one generation should be absolutely indentical with that of the preceding generation.

Contrary to Regnault's opinion (1911.1), this very striking example of adaptive modification does not demonstrate the Lamarckian principle until it is shown that such modifications are inherited.

HARMONIC OR CONFLICTING INFLUENCE OF THE FOUR FACTORS OF EVOLUTION

It is clear from the foregoing and from other examples that will be given that heredity may predispose allometric adaptations which may be developed, intensified, and more or less perfected by ontogeny, by physical environment, and by life environment, or the very reverse. The internal and the external tendencies, if all in the same direction, result in the maximum development of a given

biocharacter. In the above example of the evolution of a saltatory (leaping) type of quadruped such as the kangaroo, favorable individual exercise (ontogeny) may carry a hereditary predisposition a little beyond the normal, say from A to B. Thus the saltatory quadruped may be born with a short femur and a long tibia, the normal length of which is A. By the habit of long leaping this tibia may be lengthened to B. In nature this long leaping may have a deleterious effect on other parts of the animal or on its progeny, in which case natural selection would tend to bring the tibia of the jumper back to A. Or long leaping may be beneficial both in the avoidance of enemies and the procurement of food and not deleterious to offspring, in which case all individuals will rise to B in innumerable generations until finally natural selection will bring heredity up to B. This illustration affords an example of the relation between ontogeny and heredity that is established in that form of survival of the fittest that is known as organic or coincident selection, a theory simultaneously proposed by Osborn, Baldwin, and L. Morgan.

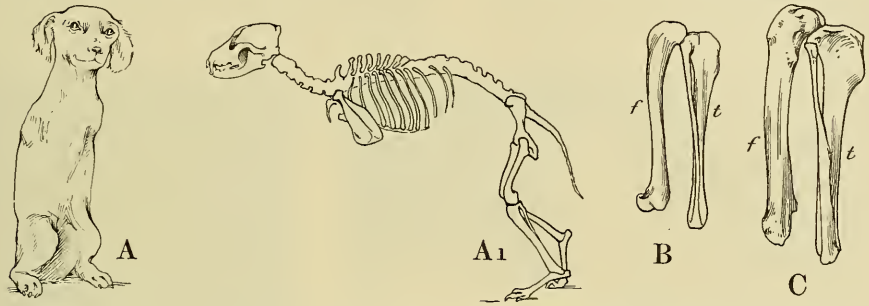


FIGURE 753.—Femur of dog, normal and as modified by amputation or congenital absence of the fore limb

A, Dog congenitally devoid of fore limbs. A^1, Skeleton of the same animal, showing the proportional enlargement of the hind limb and elongation of the femur; after Regnault, 1911. B, Normal femur, tibia, and fibula of dog. C, Femur, tibia, and fibula of a dog whose fore limbs were amputated. B and C after Fuld, 1901. All one-ninth natural size.

ONTOGENETIC ALLOMETRONS EXPERIMENTALLY INFLUENCED BY CHANGES OF ENVIRONMENT

Certain features of proportion are highly sensitive to environment. The fine, narrow hoofs of the Arab horse, for example, are developed only in reaction to the hard rocky or sandy soil of semidesert regions. If the animal is transferred to the bottom lands or grassy meadows of a humid region its hoofs become broader and flatter. Doubtless all the proportions of the body are subject, either directly or indirectly, to similar ontogenetic modifications brought about by changes of environment.

GERMINAL ALLOMETRONS: PRENATAL, ADOLESCENT, ADULT

Allen (1894.1, p. 234) observes that in *Neotoma micropus* there is an incessant change in the general proportions of the skull coordinated with growth, due mainly to the lengthening of the several skull segments without a corresponding relative increase in the breadth of the skull. *Neotoma* exhibits a progressive dolichopy and dolichocephaly in ontogeny. The development of the skull of *Neotoma* exhibits a different ratio in each of the eighteen points measured, just as the evolution of the titanothere skull exhibits a different ratio and index in every bone measured. In passing from adolescence to senility proportions wholly ontogenetic may readily be mistaken for differences of subspecific or even specific value. In a very large series of crania examined, selected from localities less than 25 miles apart, subject to similar environmental conditions, Allen observed, in addition to the ontogenetic allometrons, a large amount of individual variation both in the form and in the relative size of every element in the adult skull. He says as to size that there are dwarfs and giants. It is still difficult to determine how far this apparently spontaneous variability is actually due to environmental, ontogenetic, or germinal influence and how far to life-environmental influence.

A Darwinian interpretation of the evolution of the skull of *Neotoma* under the hypothesis of organic selection would be that the progressive elongation of the face (dolichopy) and the skull (dolichocephaly) is attributable to the combined action of natural selection of heritable fluctuations with ontogenetic modifications (allometrons due to feeding habits), on the theory that all germinal variations favoring length of the face and the head are better adapted to the feeding habits of *Neotoma* and thus would favor survival. Thus congenitally elongate skulls which in course of individual mechanical development most rapidly responded to the process of individual adaptation and to the upbending of the face upon the cranium would tend in the long run to be selected. To similar hypothetical coincidence of germinal variation, of selection, and of ontogeny might be theoretically attributed the disharmonic evolution of all the different parts of the skull.

ONTOGENETIC ALLOMETRONS INFLUENCED BY GLANDULAR INTERNAL SECRETIONS, ENZYMES, AND OTHER ORGANIC CATALYZERS

The normal hereditary proportions of the skeleton as well as of all parts of the animal body are sustained through causes of two kinds: first, normal heredity, ontogeny, physical environment, and life environment—that is, tetraplasy, the principle fully explained above; second, normal interactions between all parts of the body, probably included in tetraplasy. These normal interactions are in part sustained by the nervous system, in part by the various kinds of physico-chemical catalyzers known as enzymes, internal secretions, including hormones (accelerators) and chalones (retarders), summarized by Osborn (1917.462, pp. 250–251), from the researches of Simpson, Ashner, Cushing, Schafer, Goodale, Lillie, as follows:

FIGURE 754.—Brachydactyly and dolichodactyly

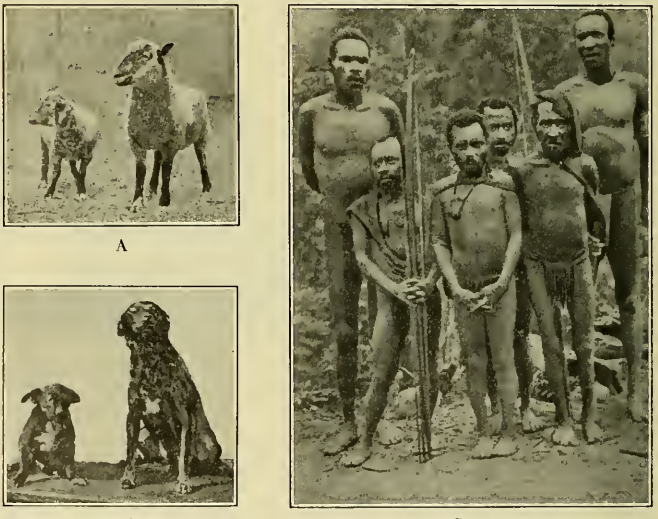
A, Brachydactyly (short-fingeredness) due to germinal saltation—that is, congenital; after Drinkwater. B, Brachydactyly that is not congenital but developed secondarily after birth through excessive internal secretions of the pituitary gland. C, Dolichodactyly (long-fingeredness) [developed after birth, attributed to abnormally insufficient secretions of the pituitary gland. B and C after Cushing, 1912.1.

These include many changes of proportion in mammals, which are not known to have a selective survival value. We may instance in man, for example, the long-head form (doliochocephaly) and the broad-head form (brachycephaly), or the long-fingered form (dolichodactyly) and the short-fingered form (brachydactyly), which have been interpreted as congenital characters appearing at birth and tending to be transmitted to offspring. Brachydactyly may be transmitted through several generations, but until recently no one has suggested what may be its possible cause.

It has now been found [Cushing, 1912.1, pp. 253, 256] that both the short-fingered condition and the long-fingered condition may be induced during the lifetime of the individual in a previously healthy and normal pair of hands by a diseased or injured condition of the pituitary body at the base of the brain. If the secretions of the pituitary are abnormally active (hyperpituitarism) the hand becomes broad and the fingers stumpy (fig. 118, *B*). If the secretions of the pituitary are abnormally reduced (hypopituitarism) the fingers become tapering and slender (fig. 118, *C*). Thus in a most remarkable manner the internal secretions of a very ancient ductless gland, attached to the brain and originating in the roof of the mouth in our most remote fishlike ancestors, affect the proportions both of flesh and bones in the fingers, as well as the proportions of many other parts of the body.

Whether this is a mere coincidence of a heredity chromatin congenital character with a mere bodily chemical messenger character it would be premature to say. It certainly appears that chemical interactions from the pituitary body are connected with the normal and abnormal development of proportions in distant parts of the body.

Allometrons, as shown above, are partly examples of biocharacter velocity. Some of the above phenomena of abnormal interaction in the organism may give us an insight into the possible causes of slow or rapid movement, of acceleration or retardation, in the origin of allometrons. These internal secretions may be connected with the fact that one proportion is retarded, as if suffering from inertia, while a conjoining proportion biocharacter is full of life and velocity, accelerated, like the alert soldier in the regiment. Whether or not internal secretions prove to be among the causes of the evolution of proportion, they are certainly among the causes of normal and abnormal development of proportion. Theoretically it is conceivable, as suggested by Cunningham (1908.1), that since hormones and chalones determine the rate of development of many organs they may



A B C

FIGURE 755.—Examples of dwarfing due to removal or abnormal functioning of certain glands

Harmonic and disharmonic alterations of proportion in mammals due to removal of the thyroid, parathyroid, pituitary, and other glands. A (right), Normal sheep of fourteen months; (left) sheep at the same age from which the thyroid and parathyroids were removed at the age of two months; after Sutherland Simpson. B (right), Normal dog of twelve months; (left) a dog of the same age and litter from which the pituitary gland was removed at the age of two months; after Aschner. C, Dwarfed macrocephalic pigmies of the hills compared with tall microcephalic plains men of west-central New Guinea; after Rawling. The question arises whether the dwarfing and macrocephaly of the pigmies may not be due to abnormal interactions (internal secretions) of certain glands like the thyroid.

also act upon the physico-chemical messengers to the germ cells, the activities of which correspond potentially with certain activities of the body cells (Osborn, 1917.462, pp. 77–78).

GERMINAL (?) ALLOMETRONS INFLUENCED BY ORGANIC CATALYZERS

There is no evidence at present that germinal predispositions of proportion are influenced by the hormones and chalones which from the above observations are shown to exert so profound an influence on bodily proportions. This can be tested only by very careful experimental work. One reason for believing that the heredity germ may be influenced in this manner is that it is the germinal or chromatin material of the body cells which responds to these organic catalyzers, as shown in the transplantation experiments of the placing of the ovary into the male body and the testes into the female body, which results in the internal secretions from these glands evoking the male characteristics in the chromatin of the female body cells and female characteristics in the chromatin of the male body cells.

These latent characters can reside only in the germ chromatin. Consequently in the germ chromatin of the germ cells proper there may be possible influences of interaction awaiting discovery through experiment. Such discovery would lend support to the tetrakinetic theory.

SUMMARY OF THEORETIC CAUSES OF EVOLUTION

EVIDENCE AGAINST THE LAMARCKIAN PRINCIPLE

The balance of evidence in titanothere evolution is decidedly against the Lamarckian principle of the inheritance of acquired characters, which was so strongly advocated, from paleontologic and mechanical data, by Cope. Neither the mode of initiation of allometrons nor that of rectigradations, when carefully analyzed, appears to sustain this principle. Though it is a convenient explanation of the development and degeneration of certain organs it does not account for all origins nor for most of the adaptations of proportion.

EVIDENCE AGAINST THE THEORY OF SELECTION OF MINUTE VARIATIONS

The evidence is also strongly against Darwin's hypothesis of the selection of minute variations as of survival value. The chief counter evidence is that new characters (rectigradations) and new proportions (allometrons) do not arise by chance but from some undiscovered definite orthogenetic principle that affects the germ.

EVIDENCE FAVORABLE TO THE SELECTION OF CERTAIN FLUCTUATIONS

The Darwinian principle, on the other hand, affords the most reasonable hypothesis we have to offer at present of the evolution of those larger proportions that have a distinct survival value—for example, the length of neck of the giraffe, the length of limbs of the unborn colt. Acceleration of adult limb proportions into fetal stages, to protect the young at birth, affords the best example of the survival value of germinal fluctuating characters and the strongest refutation of the Lamarckian hypothesis.

UNKNOWN CAUSES OF THE ORIGIN OF RECTIGRADATIONS

We are wholly at a loss to advance any explanation of the causes of rectigradations, of the orthogenetic appearance of horn rudiments on the head, or of cuspules on the teeth. Although these new characters arise independently in different phyla, thus pointing to some kind of germinal predetermination or predisposition, they do not indicate an internal perfecting tendency, because they are timed with reference to external-internal reactions. Consequently there appears to be some kind of interaction between environment, habit, and the time of appearance of these new organs; but we have no inkling as to what this relation is—whether, in fact, it is causal unless it consists of some kind of physico-chemical interaction.

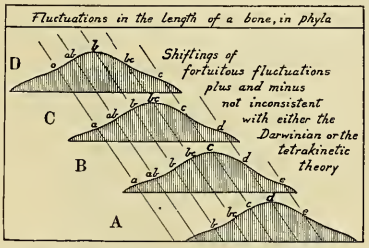


FIGURE 756.—Theoretic selection of fluctuations of proportion

Gradual shifting of proportions (*d*, *c*, *bc*, *b*, as of length of neck) in successive generations. Showing the shifting of the fluctuations of frequency in a series of characters (*a*–*e*). In a lower geologic stage (A) *d* is the most frequent character; in the next higher geologic stage (B) *c* is the most frequent character; in the next higher stage (C) *bc* is the most frequent character; in the highest stage (D) *b* is the most frequent character. This shifting is consistent with the Lamarckian, the Darwinian, or the tetrakinetic theory.

NECESSITY OF EXPERIMENT ON THE TETRAKINETIC PRINCIPLE

The tetrakinetic principle is a working hypothesis or line of suggestion as to a possible relation between the external energies of the environment and the body and the internal energies of the development and evolution of the germ. That some such causal relation exists is faintly indicated by the modes of evolution both of rectigradations and of certain proportions. As there are certain energizers in the body, catalytic messengers that hasten the development of one organ and retard the development of another, we may now obtain a glimpse of what may possibly

prove to be one of the real causes of evolution—the evolution not of the organs themselves but of the energizing chemical or physical messengers that control ontogenetic or phylogenetic velocity.

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SECTION 2. NATURAL SELECTION IN MAMMALS; CAUSES OF THE EXTINCTION OF THE TITANOTHERES AND OTHER QUADRUPEDS

In section 1 of this chapter we have treated the origin and evolution of single biocharacters, studied in the light of the Lamarckian, the Darwinian (through natural selection), and the tetrakinetic theories. In section 2 we shall consider the mammals as a whole, inquire as to the causes of their survival and extinction, and determine how far these processes are attributable to variations and fluctuations in single biocharacters and how far to the combinations of biocharacters that make up organisms.

EXTINCTION OF FAUNAS IN THE AGE OF MAMMALS

The sudden extinction of the titanotheres is one of the most striking phenomena of the age of mammals; it has generally been dismissed in a few words, but it is by no means so simple as it at first appears, because it seems to call into question all the laws of natural selection and the relation of these laws to various degrees of fitness or adaptation.

Among the more general questions of titanothere family evolution are (1) causes favoring increase in size, increase in specialization, and multiplication of the titanotheres; (2) causes bringing about diminution in size, arrest of specialization, diminution of number, and elimination of the phyla; (3) causes terminating in the extinction of the family.

The great law of mammalian adaptation through the elimination of the least adaptive becomes less sweeping in its effects as geologic time advances and the Mammalia become more highly perfected. Thus extinction is neither on the same grand zoologic scale nor chiefly due to the same causes through the successive geologic epochs of the Tertiary period. During the middle of the Eocene epoch extinction is chiefly that of inadaptive orders of archaic mammals; in the late Eocene and through Oligocene time extinction is

preeminently that of inadaptive families. Miocene time completes the elimination of inadaptive families and is broadly characterized by the extinction of inadaptive genera, a process which continues throughout Pliocene time. The especial feature of Pleistocene extinction is the ruthless and world-wide regional extermination (as distinguished from extinction) of certain highly adaptive mammals, including both genera and species, over great regions of the world.

Eocene extinction of orders appears to be due chiefly to the competition between lower and higher orders of mammals—that is, between mammals respectively more or less adaptive in intelligence and in skeletal and dental structure. In Oligocene time there a dying tree, decay in one branch after another and finally disappear entirely; or a very flourishing order like the Perissodactyla of lower Oligocene time, with its nine or more families, may be cut down to three families in a comparatively brief geologic period, and its world-wide geographic distribution may narrow down to a few favorable regions. (See fig. 757.)

EXTINCTION OF BOTH THE ADAPTIVE AND THE INADAPTIVE

Some obviously inadaptive zoologic branches, such as the titanotheres, may be cut off, and again some highly adaptive and resourceful animals, such as the horses of the Pleistocene, may yield to new dangers.

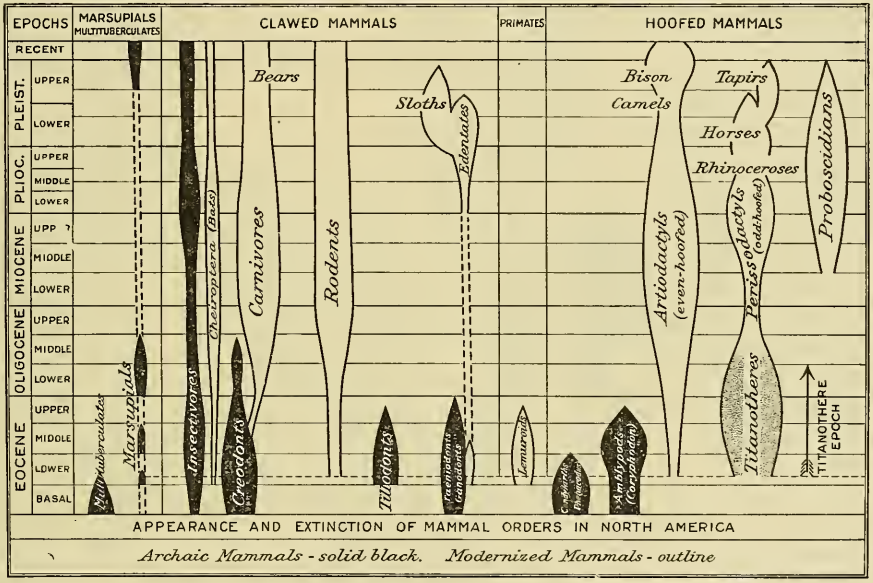

FIGURE 757.—Extinction of archaic mammals

Titanothere epoch dotted. Struggle for existence between the archaic (solid black) and modernized (outline) kinds of clawed and hoofed mammals. The surviving insectivores and marsupials are the only remnants of the archaic type.

occurred more distinctly the first fatal effects of the inadaptation of quadrupeds to environmental changes in living conditions, especially to changes in plant life. In Miocene and Pliocene time there occurred as a cumulative process the survival of the forms best adapted to the flora of the open and increasingly arid regions of the plains and uplands. In Pleistocene time all the direct and incidental effects of cold secular changes of climate appear to be the chief causes of extinction.

GRADUAL OR SUDDEN EXTINCTION

Even in immense periods of geologic time, extinction, preceded by regional extermination, may be extremely gradual or it may appear to be sudden or even cataclysmal, as it seems to have been with the titanotheres. A once flourishing order like the Amblypoda may, like

Adaptation is constantly varying in kind. Among the living races of Africa, for example, a continent which to-day gives us the closest parallel with Tertiary conditions of North America, we observe that elimination is constantly standardizing mammals through destruction of the least adaptive individuals and by this means is keeping the race up to the highest contemporary plane. Among extinct races, such as the titanotheres, we observe that elimination is pruning off the most specialized phyla of all grades, especially those which exhibit the most extreme specialization. Each of these geologic phyla was subjected to competition as a whole with other phyla, which may have evolved contemporaneously; and elimination is the death penalty of the relative inadaptation of a phylum as a whole, inadaptation either to present or to changing environment.

Changes of environment are almost infinitely complex. Mammals which from various causes may be perfectly, even exquisitely adapted in nine hundred and ninety-nine out of a thousand biocharacters may be suddenly cut off through inadaptation in one remaining biocharacter; for example, through nonimmunity to certain infectious diseases (Smith, T., 1912.1) or through deficiency of a single organ.

with diminution, impoverishment of numbers; teleologically, from the standpoint of adaptation, it is the arbiter of the fitness of whole phyla of organisms and their success in reproduction, the crucial test lying in the adaptation or inadaptation of correlated parts of the individual animals composing each phylum or in the collective capacity of the phylum as a whole to maintain itself.

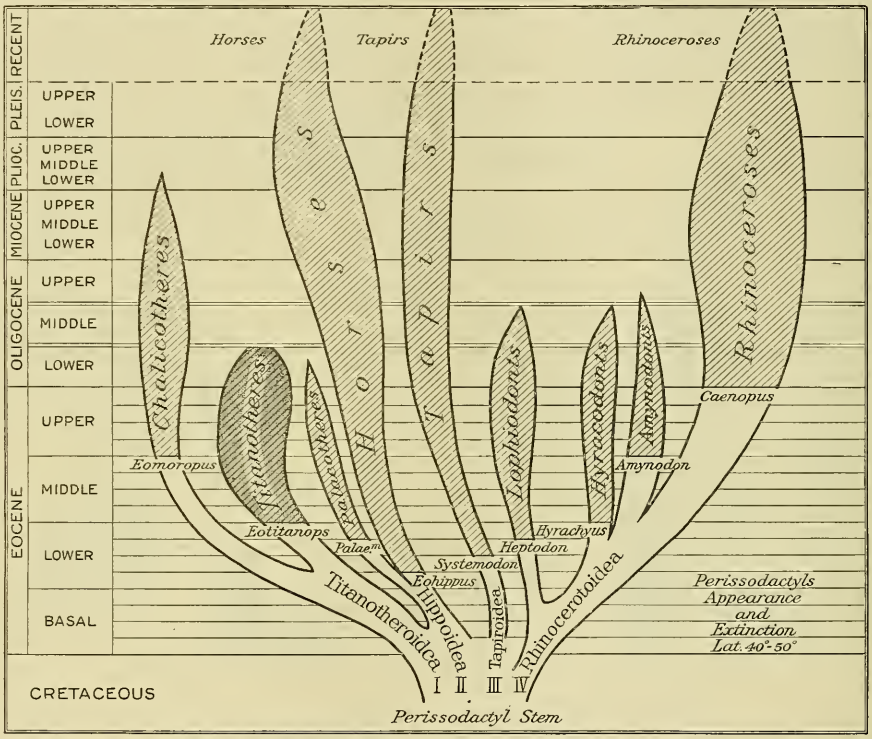

FIGURE 758.—Affinities and duration of nine families of Perissodactyla

Extinction of titanotheres (dotted). The titanotheres play a part in the early history of the order. Their period of extinction is coincident with that of the supposed aquatic rhinoceroses known as amynodonts and that of the light-limbed cursorial rhinoceroses known as hyracodonts. These animals possessed the adaptive rhinoceros-like tooth structure, yet they became extinct coincidently with the titanotheres, which were provided with cone-and-crescent grinding teeth. The family of chalicotheres, which had cone-and-crescent teeth like those of the titanotheres, survived until late Pliocene time.

PHASES OF EXTINCTION

The process of extinction usually presents three phases, as follows: (1) Numerical diminution, local in its effects; (2) regional extermination or disappearance, local in effect; (3) extinction of certain races in all parts of the world. These phases are apt to be cumulative—that is, numerical diminution is apt to lead to regional extermination through a series of causes which may finally lead to world-wide extinction. Geographically extinction may be local, continental, or world-wide; numerically it may begin

MULTIPLE CAUSES OF EXTINCTION

The first generalization that will be drawn from the broad comparative study made by the author is that there are as many causes and modes of extinction as there are vulnerable points in the structure, functions, habits, and life development of organisms, and as there are changes and vicissitudes of environment; in other words, the causes of elimination of individuals are almost infinitely varied. Whenever the rate of elimination exceeds the rate of reproduction there follows numerical diminution, which may lead to

extinction. A second broad generalization is that unfavorable effects are cumulative—that is, mammals are so closely adjusted to their environment as a whole that one series of unfavorable conditions seems to lead to or to induce another series of unfavorable conditions, and the process of numerical diminution is intensified.

Life development proceeds under the law of tetraplasy; consequently we look for the causes of extinction in the four tetrakinetic centers of capturing, storing, realizing, and reproducing vital energy, namely,

1. Heredity: the germ, germ evolution; reproduction.
2. Ontogeny: the body, habits and use, modifications, plasticity.
3. Physical environment: geologic, climatic.
4. Life environment: plants, animals.

The older historic classification of these causes is as follows:

I. Environmental, external causes:
   1. Geologic and physiographic changes of land masses and their connections.
   2. Climatic, periodic changes, secular cold, heat, moisture, etc.
   3. Biotic changes in environing plant, insect, bird, and mammal life.

II. Internal causes:
   4. The law of natural selection. Survival value of single characters. Degrees of survival value in systematic divisions. Survival value of minute variations in single characters. Adaptation and inadaptation in size, in certain organs, in intelligence, in reproduction, in plasticity or accommodation, in immunity to disease, in specialization in the trend of development, in the potentiality of further evolution, etc.

THE LAW OF NATURAL SELECTION

In studying the law of natural selection we have to view it in three aspects, as follows:

1. Selection as it concerns the origin, rise, development, competition, decline, and disappearance of each of the phyla of the titanotheres, for example, and finally of the family as a whole.

2. Selection as it concerns each of the organs that compose the individual titanotheres, their rise, development, decline, and disappearance.

3. Selection as it concerns or is supposed to concern each of the "Single characters" (biocharacters) of which these various organs are composed.

The theory of natural selection was originally stated independently by Darwin and Wallace.[63] Darwin[64] writes:

Can it be doubted that * * * any minute variation in structure, habits, or instincts adapting that individual better to the new conditions would tell upon its vigor and health? In the struggle it would have a better chance of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better chance.

Wallace[65] writes:

All the variations from the typical form of a species must have some definite effect, however slight, on the habits or capacities of the individuals. * * * If, on the other hand, any species should produce a variety having slightly increased powers of preserving existence, that variety must inevitably in time acquire a superiority in numbers. * * * The variety would now have replaced the species, of which it would be a more perfectly developed and more highly organized form. It would be in all respects better adapted to secure its safety and to prolong its individual existence and that of the race.

From 1858 until to-day one link in the Darwin-Wallace chain of thought has been a contested point in the theory of natural selection. It may be paraphrased thus:

Any minute heritable or germinal variation, be it ever so slight, which better adapts an individual to new conditions will give that individual and those of its offspring which inherit the variation a better chance of survival. Or, stated more briefly and in more modern terms: Germinal variations, be they ever so minute or slight, have a chance of being preserved and accumulated if they have adaptive or survival value.

As shown in section 1 of this chapter, very careful examination of the actual examples cited by Darwin to illustrate his meaning demonstrates that under "minute variations" he had in mind two kinds of variation, which we now distinguish as follows:

1. Minute individual variations, heritable, corresponding closely with the "mutations of De Vries.' These Darwin believed to be the chief cause of evolution.

2. Variations of proportion, now known as fluctuations, as in Darwin's explanation of the origin of the long neck of the giraffe, where he observes that any increase in the length of the neck of a giraffe would increase the animal's chance of survival in times of drought. The evidence for these hypotheses will now be reexamined, and the conclusions regarding natural selection will be summed up at the end of this chapter. These hypotheses were also examined at the end of section 1, especially in relation to the principle of tetraplasy and the tetrakinetic theory.

Does the actual order of evolution of the titanotheres favor the original Darwin-Wallace hypothesis? Do these animals evolve in the Darwin-Wallace way?

The independent development of hundreds if not thousands of distinct characters in different parts of the individual titanotheres has put before us with crystalline clearness this crucial test of the Darwin-Wallace theory of selection—namely, what observable

[63] Darwin, Charles, and Wallace, A. R., On the tendency of species to form varieties and on the perpetuation of varieties and species by natural means of selection: Linnean Soc. (Zoology) Jour. Proc., vol. 3, pp. 45–62, London, August, 1858.

[64] Darwin, Charles, Extract from an unpublished work on species, consisting of a portion of a chapter entitled "On the variation of organic beings in a state of nature; on the natural means of selection; on the comparison of domestic races and true species": Idem, pp. 46–50. Expanded and published as "On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life," 502 pp., London, John Murray, November, 1859.

[65] Wallace, A. R., On the tendency of varieties to depart indefinitely from the original type: Idem, pp. 53–62, reprinted with slight changes in "Contributions to the theory of natural selection," London, Macmillan & Co., 1870.

influence has natural selection on the origin and transformation of biocharacters, on rectigradation and proportion? What degrees of heritable variation in single characters have a survival value that can be proved by observation or experiment?

To answer this question finally it is necessary, first, to consider the laws of survival and elimination acting upon quadrupeds as a whole. These laws have been made the subject of a long special investigation by the author for this monograph, the results of which were published in 1906 in a paper entitled "The causes of extinction of mammals" (1906.287). Later results were published in 1910 in "The age of mammals in Europe and North America" (1910.346).

HISTORY OF OPINION

Although the main trend of the present inquiry as to the environmental and the internal causes of extinction had been suggested by the middle of the nineteenth century, discovery and observation since Lyell's and Darwin's time furnish new material for induction both as to the environmental and the internal causes of extinction. The true method of inquiry is to make close and continuous comparison of the present with past ages, based on the uniformitarian doctrines of Lyell and Darwin. Although we know few positive cases of natural extinction in our times, we must study all possible causes of numerical diminution, for we have every reason to believe, with Darwin, that numerical diminution is one of the highroads to actual extinction. The conception of the similarity of the past and present causes of survival and of the numerous internal causes of variation, development, and decline only gradually took its modern form.

CATACLYSMAL HYPOTHESES

Whewell (1837.1) clearly set forth the history of opinion between 1796, the Buffon-Cuvier period, and 1837, the year of the publication of his "History of the inductive sciences."

Buffon (1749.1), in commenting on the giant extinct fauna of northern Asia and Siberia, pointed out that parts of the globe now submerged were formerly elevated; he adumbrated the idea of the separation of faunas, such as the mammoths of Siberia and America, by continental depression, which resulted in the submergence of old migration routes. He attributed the disappearance of these animals from the north partly to refrigeration and partly to migration toward the south.

Cuvier (1825.1) more fully developed the cataclysmal hypotheses of regional extermination through submergence and through excessive refrigeration. In his "Discours" he observes:

> Let us suppose that a great invasion of the sea covers with a mass of sand or other deposits the continent of Australia; it would bury the carcasses of the kangaroos, wombats, dasyures, bandicoots, flying phalangers, as well as of the duckbills (*Ornithorhynchus*) and spiny anteaters (*Echidna*). It would entirely destroy the species of all these animals, because none of them exist in any other country.

After advancing the hypothesis that Australia thus depopulated might again be populated from Asia, he continues:

> To carry the hypothesis still further, after the Asiatic animals had migrated into Australia let us imagine that a second revolution destroyed Asia, the original home of these animals.

In other words, Cuvier believed in the hypothesis of a total depopulation of a continent through a great and sudden physical revolution. This was in keeping with the cataclysmal geologic theories of the time. He explained the repopulation of continents through migration from other continents in which life had persisted. This idea was taken up by Lyell.

D'Orbigny appeared as a disciple of Cuvier in his travels in South America. He writes:

> I was in a position to study the effects of inundations on the mammals of the province of Moxos (Bolivia), where these inundations are periodical, and I am certain that there the animals instinctively fly from the fluvial tide and take refuge in places further removed from the water and on pieces of high ground, where they find themselves momentarily congregated together. Ruminants sometimes die for want of food under such circumstances, and the natives mention certain years when this has occurred, but their bodies remain far from the rivers on small plateaux, or in the depths of the forests.

In summing up his results as to the destruction of the Pampean Pleistocene fauna D'Orbigny (1835.1) says that it is to the sudden rise of the Cordilleras he attributes the sudden movement of the sea, which invaded the continent all at once, carried off and overwhelmed the mastodons which inhabited the eastern flanks of the Bolivian Cordillera, the megatheriums, megalonyxes, and the multitude of animals daily being discovered in the caverns and the fissures of the mountains of Brazil—all the species, in fact, which are extinct. Again he observes:

> My final conclusion from the geological facts I observed in America is that there was a perfect coincidence between the upheaval of the Cordilleras and the destruction of the great race of animals and the great deposit of Pampas mud.

The stable continents, North America and Africa, underwent moderate fluctuations of land area in the Tertiary period as compared with the highly unstable continents of Europe, Australia, and the southern half of South America. Europe was the scene of alternating marine and fresh-water conditions, of varying coast lines, of insular and archipelagic land masses—changes which are all to be more seriously studied in connection with extinction than they have been heretofore.

It must be stated at once that the grand phenomena of extinction in unstable Europe from basal Eocene to Pliocene time broadly coincide with those observed in

the stable continent of America. This very striking fact shows, first, how cautious we must be in connecting extinction directly with physiographic changes; second, that extinction from internal causes or through competition with other species is more manifold than extinction through external causes or the struggle with environment.

Wallace (1876.1) discussed the extinction of the large Pliocene and early Pleistocene mammals of Australia chiefly from the standpoint of a physiographer—that is, he attributed Australian extinction chiefly to the increased competition, or struggle for existence, caused by the progressively contracted land area due to subsidence; also to possible glacial conditions.

The most recent advocate of this now abandoned cataclysmal hypothesis is Howorth. In his interesting and encyclopedic work "The mammoth and the flood" (Howorth, 1887.7, pp. xvii–xviii) he marshals a large number of facts in support of the hypothesis of widely destructive floods both in Asia and South America in Pleistocene time. He observes:

> These facts, I claim, prove several conclusions. They prove that a very great catastrophe or cataclysm occurred at the close of the Mammoth period, by which that animal, with its companions, were overwhelmed over a very large part of the earth's surface. Secondly, that this catastrophe involved a very widespread flood of water, which not only killed the animals but also buried them under continuous beds of loam or gravel. Thirdly, that the same catastrophe was accompanied by a very great and sudden change of climate in Siberia, by which the animals which had previously lived in fairly temperate conditions were frozen in their flesh under ground and have remained frozen ever since.

UNIFORMITARIAN THEORIES

LYELL ON EXTINCTION

Development of opinion.—Under the influence of the geologist Hutton the first note for modern methods of explanation and research as to the causes of extinction was struck by Lyell (1830.7).

Lyell's remarkable discussions of "changes of the organic world now in progress" and their bearing on the phenomena of life in geologic times will be found in the first edition of his "Principles of geology" (1830.1, vol. 2), a volume which was dedicated December 8, 1831, and published in January, 1832. Darwin departed on his voyage December 27, 1831, and took Lyell's work with him; he was profoundly influenced by it.

Lyell himself had been greatly influenced by Buffon's theories as to the destructive action of physiographic and climatic changes and by the uniformitarianism of Lamarck; also by Cuvier in respect to the repopulation of devastated land areas by migration, although in other respects he was an archopponent of Cuvier's cataclysmal hypotheses.

The following citations from Lyell's work, volume 2, chapter 10, give a clear insight into his opinions at that time:

> [*Centers of creation.*]—For we assume, on grounds before stated [chapter 8] that the original stock of each species is introduced into one spot of the earth only, and, consequently, no species can be at once indigenous in the Arctic and Antarctic circles [p. 170]. * * * The following may, perhaps, be reconcilable with known facts: Each species may have had its origin in a single pair, or individual, where an individual was sufficient, and species may have been created in succession at such times and in such places as to enable them to multiply and endure for an appointed period, and occupy an appointed space on the globe [p. 124]. * * * Now this congregating, in a small space, of many peculiar species would give an appearance of centers or foci of creation, as they have been termed, as if there were favorite points where the creative energy has been in greater action than in others and where the numbers of peculiar organic beings have consequently become more considerable [p. 126].
>
> [*Physiographic changes and accommodation.*]—Each change in the physical geography of large regions must occasion the extinction of species [p. 158]. * * * Species we have stated are, in general, local, some being confined to extremely small spots and depending for their existence on a combination of causes which, if they are to be met with elsewhere, occur only in some very remote region. Hence it must happen that when the nature of these localities is changed the species will perish; for it will rarely happen that the cause which alters the character of the district will afford new facilities to the species to establish itself elsewhere [p. 166]. * * * If, therefore, we admit incessant fluctuations in the physical geography, we must, at the same time, concede the successive extinction of terrestrial and aquatic species to be part of the economy of our system [p. 168]. * * * To pursue this train of reasoning farther is unnecessary; the reader has only to reflect on what we have said of the habitations and the stations of organic beings in general; * * * he will immediately perceive that, amidst the vicissitudes of the earth's surface, species can not be immortal but must perish one after the other, like the individuals which compose them. There is no possibility of escaping from this conclusion, without resorting to some hypothesis as violent as that of Lamarck, who imagined, as we have before seen, that species are each of them endowed with indefinite powers of modifying their organization, in conformity to the endless changes of circumstances to which they are exposed [p. 169]. * * * But the power of accommodation to new circumstances is great in certain species and might enable many to pass from one zone to another, if the mean annual heat of the atmosphere and the ocean were greatly altered [p. 171]. * * * This argument is applicable not merely to climate, but to any other cause of mutation. However slowly a lake may be converted into a marsh, or a marsh into a meadow, it is evident that before the lacustrine plants can acquire the power of living in marshes, or the marsh plants of living in a less humid soil, other species, already existing in the region and fitted for these several stations, will intrude and keep possession of the ground [p. 174]. * * * A faint image of the certain doom of a species less fitted to struggle with some new condition in a region which it previously inhabited and where it has to contend with a more vigorous species is presented by the extirpation of savage tribes of men by the advancing colony of some civilized nation. In this case the contest is merely between two different races, each gifted with equal capacities of improvement—between two varieties, moreover, of a species which exceeds all others in its aptitude to accommodate its habits to the most extraordinary variations of circumstances [p. 175].
>
> [*Climate.*]—Some of the effects which must attend every general alteration of climate are sufficiently peculiar to claim a separate consideration before concluding the present chapter

[p. 169]. * * * We have before stated that, during seasons of extraordinary severity, many northern birds and, in some countries, many quadrupeds migrate southwards. If these cold seasons were to become frequent, in consequence of a gradual and general refrigeration of the atmosphere, such migrations would be more and more regular, until, at length, many animals now confined to the Arctic regions would become the tenants of the temperate zone; while the inhabitants of the latter would approach nearer to the Equator [p. 169]. * * * But although some species might thus be preserved, every great change of climate must be fatal to many which can find no place of retreat, when their original habitations become unfit for them. For if the general temperature be on the rise, then is there no cooler region whither the polar species can take refuge; if it be on the decline, then the animals and plants previously established between the Tropics have no resource [p. 170]. * * * Let us now consider more particularly the effect of vicissitudes of climate in causing one species to give way before the increasing numbers of some other [p. 172]. * * * That they would be supplanted by other species at each variation of climate may be inferred from what we have before said of the known local exterminations of species which have resulted from the multiplication of others. Some minute insect, perhaps, might be the cause of destruction to the huge and powerful elephant [p. 174].

[*Moving sands.*]—If we attribute the origin of a great part of the desert of Africa to the gradual progress of moving sands, driven eastward by the westerly winds, we may safely infer that a variety of species must have been annihilated by this cause alone. The sand flood has been inundating, from time immemorial, the rich lands on the west of the Nile, and we have only to multiply this effect a sufficient number of times in order to understand how, in the lapse of ages, a whole group of terrestrial animals and plants may become extinct [p. 166]. * * * In a small portion of so vast a space, we may infer, from analogy, that there were many peculiar species of plants and animals which must have been banished by the sand, and their habitations invaded by the camel and by birds and insects formed for the arid sands [p. 166]. * * * If it be imagined, for example, that the aboriginal quadrupeds, birds, and other animals of Africa emigrated in consequence of the advance of drift sand and colonized Arabia, the indigenous Arabian species must have given way before them and have been reduced in number or destroyed [p. 167].

[*Repopulation through migration.*]—So great is the instability of the earth's surface that if Nature were not continually engaged in the task of sowing seeds and colonizing animals, the depopulation of a certain portion of the habitable sea and land would in a few years be considerable [p. 158]. * * * If, therefore, the Author of Nature had not been prodigal of those numerous contrivances before alluded to, for spreading all classes of organic beings over the earth—if he had not ordained that the fluctuations of the animate and inanimate creation should be in perfect harmony with each other, it is evident that considerable spaces, now the most habitable on the globe, would soon be as devoid of life as are the Alpine snows, or the dark abysses of the ocean, or the moving sands of the Sahara [p. 159].

Summary.—Summing up Lyell's opinions of 1831 we find them remarkably modern and Darwinian, both in observation and in reasoning. The chief points as to extinction are the following: (1) The destructive effect of physiographic changes in Tertiary time (p. 308) is to be interpreted through the extinction of species at the present time; (2) temperature barriers are important factors in distribution (p. 172); (3) the destructive action of floods (p. 199) may be understood through the disappearance of large numbers of horses in South America (pp. 249, 312) and of buffaloes in India (p. 250); (4) animals may have also perished in large numbers in bogs (p. 217); (5) changes of climate induced by physiographic changes (p. 308) influence both distribution (p. 169) and competition between species (p. 172); (6) competition between related species is illustrated by that between the horse and ass, as introduced into South America; (7) competition between unrelated animals is illustrated by the unchecked increase of goats (p. 153), of asses (p. 153), of cattle and horses (pp. 152–153), and of insects (p. 320); (8) increase, however, suffers many checks, as was first noted by Buffon (p. 154); (9) there is constant competition between established species (p. 142) and newly introduced species; (10) the balance of nature (pp. 133, 138, 139) is brought to an equilibrium through the relations of plants and insects (p. 132), and unlimited increase is subject to other checks (pp. 133, 138, 139); (11) many species might be destroyed through the devastation of plant life caused by locusts (p. 137), or by the advance of sands and sandstorms in desert regions (p. 166), as illustrated in the burial of camels and other animals; (12) plagues of ants would be highly destructive of certain types of animals (p. 137). Under the influence of Lamarck, Lyell observed that extinction might be averted by "accommodation" to a new environment, but he argued that under many conditions accommodation would not be rapid enough, as Lamarck supposed, to avert extinction.

Especially interesting is Lyell's calculation (p. 183) of the time required for the extinction of one species. If the earth were divided into twenty regions of equal area one of these would about equal the dimensions of Europe and might contain a twentieth part of the million species which we would suppose to exist. In such a region one species, according to the assumed rate of mortality, would perish in 20 years, or 5 species out of 50,000 in the course of a century. In the class Mammalia it would require more than 8,000 years to lose one group in a region of the dimensions of Europe.

BALANCE OF NATURE (LYELL, DARWIN, WALLACE)

Lyell.—Referring to that subtle adjustment of the sum of all internal and external causes known as the balance of nature, Lyell (1872.1, vol. 2, pp. 455–456) observed:

Every new condition in the state of the organic or inorganic creation, a new animal or plant, an additional snow-clad mountain, any permanent change, however slight in comparison to the whole, gives rise to a new order of things and may make a material change in regard to some one or more species. Yet a swarm of locusts, or a frost of extreme intensity, or an epidemic disease may pass away without any great apparent derangement; no species may be lost, and all may soon recover their former relative numbers, because the same scourges may have

visited the region again and again, at preceding periods. Every plant that was incapable of resisting such a degree of cold, every animal which was exposed to be entirely cut off by an epidemic or by famine caused by the consumption of vegetation by the locusts, may have perished already, so that the subsequent recurrence of similar catastrophes is attended only by a temporary change.

As a geologist Lyell believed that the destructive influence of geologic and physiographic changes was extremely gradual. In 1863 (1863.7, p. 374) he observed:

It is probable that causes more general and powerful than the agency of man, alterations in climate, variations in the range of many species of animals, vertebrate and invertebrate, and of plants, geographical changes in the height, depth, and extent of land and sea, some or all of these combined, have given rise, in a vast series of years, to the annihilation not only of many large Mammalia but to the disappearance of the *Cyrena fluminalis*, once common in the rivers of Europe, and to the different range or relative abundance of other shells which we find in the European drifts.

Darwin.—The next great student of this subject was Charles Darwin. His voyage around the world (1831–1836) on the exploring ship *Beagle* (1839.1) afforded him an extraordinary opportunity of testing the theories advanced in Lyell's "Principles" as first published in the previous year (1831). Especially in the Pampean and Patagonian regions he contrasts the Buffon-Cuvier and the Lyell hypotheses in favor of the latter. He dismisses catastrophic causes and in general attributes extinction to a cessation of those world-wide conditions of life which were favorable to the larger quadrupeds in Europe, Asia, Australia, North and South America. In South America and elsewhere (1) he does not favor the extreme theory of the destructive influence of the glacial epoch, and he cites the supposed postglacial survival of *Macrauchenia* and *Mastodon*. "It could hardly have been a change of temperature," he observes (p. 170), "which at about the same time destroyed the inhabitants of tropical, temperate, and Arctic latitudes on both sides of the globe." (2) He dismisses the possibility of extinction by man; (3) also of an extended drought in South America, calling attention to the Pampean horse as an animal which could have survived a drought.

In seeking to establish a general law of extinction Darwin makes the following propositions: (1) Animals naturally increase in geometrical ratio; (2) the food supply, however, remains constant; (3) any great increase in numbers is thus impossible and must by some means be checked; (4) we are seldom able to state the cause of this check beyond saying that it is determined by some slight difference in climate, food, or the number of enemies; (5) we are therefore driven to the conclusion that causes generally quite inappreciable by us determine whether a given species shall be abundant or scanty in numbers; (6) comparative rarity is the plainest evidence of less favorable conditions of existence; (7) rarity frequently precedes extinction, and if the too rapid increase of species, even the most favored, is steadily checked, why should we feel such great astonishment at the rarity being carried a step farther to extinction?

Darwin's earlier views (1839–1845), developed from observations made during his voyage, on droughts, floods, insect life, epidemics, were more fully elaborated in connection with the publication of his theory of natural selection (1858, 1859). In his "Origin of species" (1859) he discusses more fully the checks to increase as follows: (1) Climate as directly unfavorable; (2) climate as indirectly unfavorable by favoring other forms or by increasing the number of certain competitors; (3) unchecked increase frequently followed by epidemics, possibly in part by facility of diffusion of parasites among the crowded animals; (4) finally, since a large stock of individuals, relatively to the number of enemies, is absolutely necessary for the preservation of a species, a diminished number would tend to extinction; (5) any form (p. 133) that is represented by few individuals will run a good chance of utter extinction during great fluctuations in the nature of the seasons or from a temporary increase in the number of its enemies; (6) diminution in number presents less opportunity for producing favorable variations, hence rare species will be less quickly modified or improved within any given period.

Wallace.—Wallace in his long series of contributions to the natural selection and Darwinian theory developed similar views (1858.1). In "Natural selection" (1870.1, p. 14) he observes:

To discover how the extinct species have from time to time been replaced by new ones down to the very latest geological period is the most difficult and at the same time the most interesting problem in the natural history of the earth. * * * Whenever the physical or organic conditions change, to however small an extent, some corresponding change will be produced in the flora and fauna, since, considering the severe struggle for existence and the complex relations of the various organisms, it is hardly possible that the change should not be beneficial to some species and hurtful to others.

The majority of the speculations of these great naturalists are abundantly confirmed by modern paleontology. The lines of thought and investigation developed by Lyell and Darwin are precisely those which we are pursuing to-day, but our greatly expanded knowledge of paleontologic history, of the biologic results of physiographic revolutions, of relatively sudden extinctions at the close of certain periods, of the means of the spread of epidemics by insect agencies, of the elimination of certain structural types opens up entirely new fields of actual observation and comparison for the formation of more precise and definite conclusions. In short, we are in a position to substitute for the ingenious and profound speculations of Lyell and Darwin a number of concrete examples of extinction that can certainly be traced to definite and specific causes.

ENVIRONMENTAL CAUSES OF EXTINCTION

THE PHYSICAL ENVIRONMENT

PHYSIOGRAPHIC CHANGES

In our inquiry as to the causes of extinction we may first consider those which originate with changes in the environment brought about by geographic revolutions—such changes in land masses, including elevation and subsidence, as act directly upon all the physical conditions of climate, moisture, or desiccation, changing vegetation, etc., and facilitating or restricting migration, with resulting new competitions, etc.

Base-leveling a cause of extinction.—The effects of base-leveling, or the erosion of mountainous and other land surfaces to a single peneplain, has been especially discussed by Woodworth (1894.1) and Adams (1901.7; 1904.1). Woodworth points out that the development of the peneplain, the widening of the lowlands, plains, and jungles nearly to tide level in Cretaceous time, was highly favorable to the water-loving Reptilia and unfavorable to mammalian life. New species are brought into competition when a mountain system is leveled off, thus throwing the life of its opposite slopes into the same field. The degradation of uplands has a very direct effect, since organisms suited to steep slopes and high altitudes with low temperatures must migrate, vary, or live at a disadvantage as the surface is lowered by denudation. Other things being equal, the endemic lowland forms will have an advantage over those organisms which are living under the trial of alternating environment with the added stress of contest with hitherto unmet species. Periods of base-leveling are characterized by relative stability of the land with reference to the sea, while periods of glaciation are characterized by relative instability.

Insular conditions.—The substitution of insular for archipelagic or continental conditions by subsidence has undoubtedly been a potent cause both of extermination in certain localities and of the survival of geologically ancient primitive forms (Wallace), such as Monotremata and Marsupialia, in the Australian region. It may be said at once, with Lyell, that most of the causes both of survival and extinction which prevail on continents are intensified on islands; yet on islands the phenomena are those of local extermination and modification rather than the general extinction of families and orders, which is our real subject of inquiry.

Dwarfed Pliocene and Pleistocene island life.—In the islands of Malta, Cyprus, and Crete, as explored by Miss Bate (1905.1), we have fine examples of comparatively recent insulation.

It appears probable that Cyprus became an island first, because (1) no submerged bank connects it with the mainland, and the 200-fathom line is reached within a short distance of the coast line; (2) the terrestrial fauna and avifauna include several distinct races peculiar to the island, a fact confirmed by Kobelt from his study of the recent Mollusca. The reduced existing Cyprus fauna contains a mingling of European and north African forms and shows the effects of deforestation in historic times. The largest animal on the island is the moufflon (*Ovis ophion*), 25 inches high at the shoulders; yet this is the smallest of all the wild sheep and is related to east Persian species.

The affinity of Malta to Sicily is indicated by the occurrence of two species, *Hippopotamus pentlandi* and *Elephas mnaidriensis*, in the cavern deposits of both islands. The early separation of Cyprus is indicated by the fact that *E. cypriotes* and *H. minutus* are both more primitive than the Maltese-Sicilian species. Crete also includes antelope and deer in its Pleistocene fauna.

Pleistocene extinct fauna of the Mediterranean islands

	Proboscidea (pigmy elephants)	Artiodactyla (pigmy hippopotami)
Cyprus	E. cypriotes	H. minutus.
Malta	E. melitensis, E. mnaidriensis.	H. pentlandi.
Sicily	E. mnaidriensis	H. pentlandi.
Sardinia	E. lamormorae	

The occurrence of these specifically different though apparently closely related races of small elephants and hippopotami in widely separated islands is an instance of independent development with some divergence from common ancestors.

Volcanic ash.—The comparatively recent recognition that vast areas, both in the Rocky Mountain region and in Patagonia, were the seats of deposition of volcanic dust arising from volcanic eruptions indicates that this may be considered among the means of numerical diminution if not of extermination in certain regions. There is evidence in Patagonia especially that many animals were overtaken and buried entire in volcanic dust; but this is less frequently true of the volcanic dust deposits in the Eocene of North America, where few "entire" burials have been found.

Floods.—It appears that floods have very frequently been a cause of marked diminution in number, which is a very different result from regional extermination or extinction. The instances cited by Howorth, by D'Orbigny, and by Azara (as quoted by Darwin) indicate that floods may be considered among the secondary or contributary causes of extermination.

In the summer of 1867, it is recorded, over 2,000 buffalo out of a herd of about 4,000 lost their lives in the quicksands of the River Platte while attempting to cross (Hornaday, 1889.7, p. 421). The floods and swollen rivers of Pleistocene time presented a new set of conditions.

Conclusions.—Since there is little parallel between the Eocene changes in Europe and those of western America, and a very close parallel between the phenomena of extinction in Europe and those of western America, the conclusion is inevitable that physiographic changes are not directly potent factors of extinction but are indirectly potent through the biotic changes which they induce, new types of adaptation, new forms of competition, etc.

CHANGES OF CLIMATE

We have now to consider changes in temperature and moisture as brought about by geologic and physiographic changes and as effecting in turn biotic changes—changes in the fauna and flora.

Pleistocene secular increase of cold.—The effects of secular lowering of temperature must be analyzed with some care. At first sight the original theories of extinction of Buffon and Cuvier regarding refrigeration or direct action of cold are very simple and plausible, but on examining all the instances of extinction which occurred during the Pleistocene or glacial epoch we find that this simple or obvious explanation is not the true one. To take the glacial epoch, which affords the chief illustration, it is more in general accord with the facts to say that this period originated certain new conditions of life which diminished numbers and hastened extinction. These conditions include such phenomena as deforestation, enforced migrations, overcrowding, changes of food, unfavorable conditions of mating and reproduction, new relations to enemies, and other indirect results. The reason refrigeration can not be considered alone or as a direct cause lies in the remarkable powers of plastic adaptation which many mammals, including man, exhibit to secular or regional lowering of temperature. The horse of North America became extinct during the glacial epoch, yet there is every reason to believe that its extermination was not directly connected with the Ice Age.

General phenomena.—Among the observed climatic phenomena and biotic effects of unusual cold periods are the following: Harsh or unusual conditions of life caused by snowstorms, blizzards, ice floods, diminution of food supply, limited choice of food caused by change of flora and deforestation, enforced choice of deleterious food, changes in fertility and reproduction rate, dangers to young, arrested growth, diminution in number causing diminished herds, enforced migrations, crowding southward.

Protective adaptation.—Secular cold is very slowly progressive and has generally been accompanied step by step by progressive adaptation among the mammals to resist cold. Resistance depends upon (*a*) internal-heat producing power, which is a progressive adaptation of the ascending series of mammals as distinguished from the reptiles; (*b*) acquisition of a warm external covering of wool and hair; (*c*) development of subcutaneous and other fatty layers; (*d*) power of hibernation. The well-known instances of adaptation to extreme cold among the Proboscidea (*Elephas primigenius*, woolly mammoth, *Mastodon americanus*, mastodon), rhinoceroses (*R. tichorhinus*, woolly rhinoceros), horses (*E. przewalski*), northern ruminants (Saiga antelope, Bactrian camel, Barren-Ground and Arctic caribou, musk ox) indicate again that we must not assume that refrigeration was a direct or sole cause of extinction.

Glacial and postglacial extinction.—Wallace observes (1876.1, p. 151):

> We have proof in both Europe and North America that just about the time these large animals were disappearing all the northern parts of these continents were wrapped in a mantle of ice; and we have every reason to believe that the presence of this large quantity of ice (known to have been thousands of feet if not some miles in thickness) must have acted in various ways to have produced alterations of level of the ocean as well as vast local floods, which would have combined with the excessive cold to destroy animal life.

And again (1881.1, p. 117):

> We can therefore hardly fail to be right in attributing the wonderful changes in animal and vegetable life that have occurred in Europe and North America between the Miocene period and the present day, in part at least, to the two or more cold epochs that have probably intervened. These changes consist, first, in the extinction of a whole host of the higher animal forms; and, secondly, in a complete change of types due to extinction and emigration, leading to a much greater difference between the vegetable and animal forms of the Eastern and Western hemispheres than before existed.

Wallace's views regarding glacial extinction are modified by the present four-glaciation theory. The large African-Asiatic fauna of Europe, namely, the hippopotami, the rhinoceroses, the elephants, and the mammoths, survived the first, second, and third glaciations but perished before or during the extremely severe climatic conditions of the fourth glaciation.

Frech observes (1906.1):

> The chief problem in regard to extinction is in general confined to the question whether the great climatic changes of former geological periods coincide with the great transformations of the plant and animal kingdoms. Corresponding with the fall in temperature at the close of the Tertiary in Europe is the disappearance of all the tropical and subtropical animals (tapirs, mastodons, hipparions, and the last tropical antelopes, *Protragelaphus* and *Palaeoryx*). In the Quaternary, before the advent of the [last] glacial period the last remnants of the subtropical fauna vanished from central Europe (*Hippopotamus major*, *Machaerodus*) also the tropical elephants and rhinoceroses characterized like the recent forms by a practically hairless skin. The mammoth and the Arctic rhinoceros had in their long and dense woolly coat perhaps the best protection against cold that any terrestrial animal has ever possessed. The adaptations to cold, equally well defined in large and small animals of the circumpolar fauna, presuppose a long period of time for their development. The mammoth probably existed in Siberia under conditions of temperature similar to those prevailing at the present time, before the beginning of the glacial period. The general fall in temperature was probably first marked in northern Siberia and thus it was here that conditions first became favorable for the evolution of an Arctic fauna. The general drop of 4° C. in temperature moved the

northern limit of trees further to the south. The large ruminants were thus forced southeast, southwest, and west, since the desert plateaus of central Asia shut off a retreat to the south.

By far the most impressive of all the examples of extinction known to us is this continental extermination of numerous forms of mammalian life, both carnivores and herbivores, which was contemporaneous with this great secular change of climate. It is no exaggeration to say that the faunal aspect of Australia, South America, North America, Asia, and Europe was profoundly altered as it had never been before. This alteration entirely changed the zoologic aspect of four-fifths of the earth's surface, and it is unavoidable that we should attribute it to the long series of direct and indirect changes connected with the four or five waves of advancing and retreating low temperature and moisture.

The end of the Pliocene and beginning of the Pleistocene found North America populated with the kinds of great herbivorous quadrupeds tabulated below, all of which disappeared in North America during the Ice Age, although some of them survived in other forms in South America, Europe, and Asia.

Herbivorous quadrupeds of North America that became extinct during the Ice Age

Suborder	Family	Kind or genus	Time of extinction
Artiodactyla	Camelidae	Camels, llamas	Before the end of the Kansan stage; not known after the Aftonian stage.
Perissodactyla	Equidae	Horses	Before the end of the Kansan; not known after the Aftonian except E. complicatus, which is found in Sangamon deposits.
	Tapiridae	Tapirs	Before the Wisconsin, but after or during Sangamon.
Proboscidea	Mastodontinae	Mastodons	After the Wisconsin glacial stage.
	Elephantinae	Elephants (mammoths)	Do.
Edentata	Gravigrada	Giant sloths:	
		Megalonyx	Do.
		Megatherium	Probably before the end of the Kansan stage.
		Paramylodon	Mylodon (Paramylodon) not known after the Wisconsin probably extinct during or after the Sangamon stage.
	Glyptodontia	Glyptodon	Probably became extinct in the first third of the Pleistocene, before the Kansan stage.

It would be natural to assume that extinction was directly brought about by these successive changes of temperature and moisture and the changes in the fauna and flora consequent upon the great physiographic changes; but this simple explanation is beset with many difficulties and contradictions, and the results must be analyzed with some care. In Europe the Mediterranean Sea presented a barrier to escape or migration southward, but in North America there were broad continental areas and high plateaus that afforded easy routes of migration southward and every means of escape. It is therefore more in accord with the facts to say that contemporaneous with the glacial epoch in North America there were developed certain new conditions of life that directly or indirectly resulted in extermination.

Numerical diminution in hard winters.—These phenomena have been discussed by Nehring (1890.1) in connection with the Ice Age in noting the effects of severe storms on the steppes of Russia, where animals are not protected by stretches of forest. Garman (1883.1) maintains that snow was the chief cause of the extermination of the Pleistocene species of bison and horses in North America. We owe to Seton (1909.1) a review of the observations of Munson, Spears, Bunn, Henry, and others of exceptional periods of numerical diminution on the Great Plains. Henry in 1799 (1897.1, vol. 1, p. 174, and footnote) counted "herds" of drowned and mired buffalo along the banks of Qu'Appelle River. Treacherous ice in the spring of 1801 destroyed great numbers of buffalo along the shores of Red River (Alberta); for two days and nights a continuous line of carcasses floated by. The blizzard of 1871–72 diminished the last great buffalo herd of South Dakota. In 1880 large numbers of buffalo perished in a blizzard in the same region, 50 skeletons being found together in one ravine. The hard winter of 1893 (thermometer −61° F.) killed off four-fifths of the antelope near Fort Assinniboine, Mont. Carcasses of about 900 animals, which had starved to death on account of the deep snow, were found in one ravine.

Dangers of numerical diminution.—While a sharp distinction must be drawn between actual extermination on a continent and a temporary diminution caused, for example, by cold waves, floods, or other unfavorable conditions of life, it is very important to observe, as first suggested by Darwin, that extreme diminution in numbers has as great dangers as extreme multiplication in numbers and may lead to

extermination. For example, a herd of animals may be reduced to the danger point in numbers so that they can no longer protect their young. Bell, former Acting Director of the Geological Survey of Canada, observes that the small surviving herd of woodland bison (*Bison bison athabascae* Rhoads) of British Columbia, although conserved by the Government, will probably be destroyed gradually through the killing of the calves by wolves, the bulls not being sufficiently numerous to protect the calves.

Diminished herds and inbreeding of bison.—In a paper entitled "Das allmähliche Aussterben des Wisents (*Bison bonasus* Linnaeus) im Forste von Bjelowjesha," Eugen Büchner (1895.1) gives a detailed history of the bison herd in the Bieloviejsha (or Bialowitza) forest, Province of Grodno, in Lithuania, during the present century.

A careful study of the breeding habits of the bison in the Bieloviejsha forest and elsewhere leaves no room for doubt that the present slow rate of reproduction is an abnormal condition, and that to it is due the rapid approach of the extinction which is the certain fate of the herd under consideration. This diminished fertility the author regards as a stigma of degeneration caused by inbreeding. * * * Another indication of the degenerate condition of the Bieloviejsha herd is seen in the great excess of bulls, which probably outnumber the cows two to one. This is doubtless a result of inbreeding, for Düsing (1884.1) has shown that close inbreeding, like a reduced condition of nutrition, is favorable to the production of an excess of males. * * * In conclusion, the author considers that his studies of the history of the Bieloviejsha bison leave scarcely room for doubt that inbreeding is the cause of the final extinction of most large mammals. Inbreeding must begin and lead gradually but certainly to the extinction of a species when it, through any cause, has become so reduced in numbers as to be separated into isolated colonies.

Numerical diminution of llamas.—The observations of Prichard (1902.1, pp. 132, 189, 255) in Patagonia afford an interesting instance of numerical diminution among the Camelidae.

Around the lake lay piled the skulls and bones of dead game, guanaco (*Lama huanachus*) and a few huemules (*Furcifer chilensis*). These animals come down to live on the lower ground and near unfrozen water during the cold season, and there, when the weather is particularly severe, they die in crowds. We saw their skeletons, in one or two places literally heaped one upon the other [p. 132]. * * * Again we came upon a second death place of guanaco, which made a scene strange and striking enough. There can not have been less than 500 lying there in positions forced and ungainly as the most ill-taken snapshot photograph could produce. Their long necks were outstretched, the rime of the weather upon their decaying hides, and their bone joints glistening through the wounds made by the beaks of carrion birds. They had died during the severities of the previous winter and lay literally piled one upon another [p. 189]. * * * The meaning of this I gathered from Mr. Ernest Cattle. He told me that in the winter of 1899 enormous numbers of guanaco sought Lake Argentino and died of starvation upon its shores. In the severities of winter they seek drinking places, where there are large masses of water likely to be unfrozen. The few last winters in Patagonia have been so severe as to work great havoc among the herds of guanaco [p. 255].

Numerical diminution of Sirenia.—Interesting instances of the effects of "cold waves" in a subtropical region are those cited by Bangs (1895.1) regarding the rivers of Florida, especially in the case of the manatee (*Manatus manatus*). These animals are extremely sensitive to a lowering of temperature. During the winter of 1894–95 there was an unusually cold wave followed by marked numerical diminution, several of these animals being found ashore dead.

Deforestation and secular cold.—The main natural causes of deforestation appear to be (1) extreme heat and secular desiccation; (2) periodical fires that destroy the young trees; (3) excessive browsing, which destroys the young trees; (4) excessive cold resulting in prolonged and deep snow mantling; (5) continuously frozen subsoil or tundra condition; (6) plagues of insects and other forest destroyers.

After considering the former abundant mammalian life in Alaska, Maddren (1904.1, pp. 65–66) summarizes his conclusions as follows:

I. That while remnants of the large Pleistocene mammal herds may have survived down to the Recent period and in some cases their direct descendants, as the musk ox, to the present, most of them became extinct in Alaska with the close of the Pleistocene.

II. The most rational way of explaining this extinction of animal life is by a gradual changing of the climate from more temperate conditions, permitting a forest vegetation much farther north than now, to the more severe climate of to-day, which, subduing the vegetation and thus reducing the food supply besides directly discomforting the animals themselves, has left only those forms capable of adapting themselves to the Recent conditions surviving in these regions to the present.

Influence of cold and snow on food supply and choice of food.—The death of great numbers of animals from hunger or starvation through the covering of food during the winter under heavy layers of snow is commonly observed among the large herds of some of the domesticated horses and cattle on the western plains. In fact, it is most probable that during the glacial epoch the great winter snow blankets covering the natural food were the chief cause of extinction rather than the actual influence of the cold itself.

Under these conditions horses are driven to eat food which is very deleterious to them, such as the branches of willows. Under the influence of hunger cattle and sheep will feed eagerly and indiscriminately on plants that may be injurious to them or to their young, as recorded by Chesnut and others in the United States Department of Agriculture. The indirect results of hunger may therefore be quite as effective as actual starvation.

Animals vary greatly in adaptability to new conditions caused by prolonged cold and heavy snowfall. Horses remove snow even to depths of 3 or 4 feet and find food to carry them through the winter, whereas under the same conditions cattle starve.

Influence of cold during the reproduction period.—Exceptional cold waves or unusually prolonged cold

seasons may cause a temporary loss of food supply or cause the death of the young, which in northern latitudes are usually born in spring. The diminution or loss of young from this cause might act as the first of a series of destructive effects of a progressive secular change. These may be summarized as follows from actual zoological observations [66] among the Cervidae: (1) Disturbed conditions during the conjugation (pairing, mating, rutting) period; (2) enfeebled (through hunger) condition of females during parturition period; (3) severe weather conditions, ice storms, crusted snow, prolonged wet and sleet at time of birth; (4) bulls unable to protect herds; (5) cows unable to protect young from Carnivora through starved condition, or abandoning them when attacked by wolves; (6) enfeebled and unprotected condition of quadrupeds favorable to increased food supply and consequent multiplication of cursorial and other Carnivora, especially Canidae and Felidae.

These zoological observations are to a certain extent borne out in paleontology by Andrew Leith Adams's observation (1879.1, p. 98) of the exceptionally large number of milk teeth of elephants found in certain Pleistocene deposits, which appears to indicate a high mortality of the young.

Merriam (1892.1), in what he has called the "law of temperature control," has directed attention to the physiological effects of a lowering of temperature upon diminished or increased fertility and the rate of reproduction. It is stated as follows: Temperature, by controlling reproduction, predetermines the possibilities of distribution; it fixes the limits beyond which species can not pass; it defines broad transcontinental barriers within which certain forms may thrive if other conditions permit, but outside of which they can not exist, be the other conditions never so favorable, because the sexes are not fertile.

In discussing how species are checked in their efforts to overrun the earth Merriam points out that more potent than geographic barriers are climatic barriers (as observed by Humboldt), and of these temperature is more potent than humidity. First, in 1892, Merriam attempted to show (1892.1, pp. 45–46) that the distribution of terrestrial animals is governed less by the yearly isotherm or mean annual temperature than by the total temperature during the period of reproductive activity and of growth (adolescence). This reproductive period in the Tropics extends over many months or nearly the whole year but within the Arctic Circle and summits of high mountains is of two months or less duration. Later results that Merriam (1894.1) obtained from extensive comparison of temperatures and distribution justified the belief that animals and plants (lower austral and tropical types coming from the south) are restricted in northward distribution by the total quantity of heat prevailing during the season of development and reproduction. Conversely, animals and plants (upper austral, transition, and boreal types coming from the north) are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year. Thus in the transition zone boreal and austral types mingle in the equable climate of the Pacific coast of California, whereas they are sharply separated by the inequable extremes of cold and heat of the interior continental plateau.

Lowering of temperature and diminished fertility.—The favorable influence of high temperature on fertility and reproduction is well illustrated in the early age of reproduction in tropical lands and the increase in the fertility of the human species toward the Equator, and as low temperature is thus a barrier to reproduction it is reasonable to suppose that the secular lowering of temperature may have been one among the causes of the extinction of animals during the glacial age. Thus certain mammals, although they were otherwise becoming adapted to the effects of cold and were discovering new means of feeding, may have become extinct through the subtle inhibition of fertility and the lowering of the rate of reproduction.

Increasing moisture in Temperate Zone.—Humidity, observes Merriam (1894.1) in the work cited above, is a less potent factor than temperature in limiting the distribution of the mammals of North America [that is, in cold and temperate climates]. Thus many genera adapted to restrictions of temperature zones range east and west completely across the American Continent, inhabiting alike the humid and arid subdivisions, but no genus adapted to certain restrictions of humidity ranges north and south along the temperature zones. Thus, according to Merriam, humidity governs the details of distribution of a few species of mammals within certain temperature zones; temperature establishes the great wall, and humidity establishes the lesser barriers.

This law may be understood as the direct influence of temperature and humidity respectively; the indirect or secondary influences of temperature and humidity may be entirely different. Thus Merriam's generalization would not apply to central Africa, Central America, or other tropical countries where insect and disease barriers exist which are generated and favored by high temperature and increasing moisture. Because of the connection between insect distribution and moisture in Africa, humidity is considered to be a very potent factor in the distribution of animals.

Moisture in the Equatorial Zone.—We observe that increased rainfall may have the following effects, especially upon the Herbivora: (1) It may diminish the supply of harder grasses to which certain quadrupeds

[66] Communicated by Mr. Madison Grant, secretary of the Zoological Society of New York.

had become thoroughly adapted; (2) it may introduce new poisonous or deleterious plants; (3) it may be the means of erecting new forest barriers or new forest migration tracts for certain Carnivora; (4) it may be the means of introducing new insect and other pests, as well as new insect barriers; (5) it may be the means of introducing new diseases and new insect carriers of disease.

Besides the changes in plant food that are brought about by diminished moisture, as indicated below, there are the effects of increased moisture which may be equally if not more important. Moist conditions may cause increase of certain forms of plant life deleterious to all Herbivora. Dry or moderately dry conditions, provided they are not too extreme, are generally more favorable to quadrupeds than moist conditions. The plateau and forest regions most densely populated with quadruped life, such as those of Africa, are regions of moderate rainfall and even of prolonged summer droughts. On the other hand, the regions least densely populated with mammals are those of heavy rainfall, dense forests and vegetation, such as those of the equatorial belt of South America and of Africa.

It follows that periods of secular increasing moisture, such as the warm interglacial stages of Pleistocene time in the Northern Hemisphere, may have proved unfavorable to certain large quadrupeds through increase of humidity and rise in temperature even prior to the advent of extreme cold.

Insect barriers and moisture.—It is now a matter of general observation that, especially in tropical, insect-infested countries, dry seasons result in the reduction, moist seasons in the increase of disease. Dry localities are generally favorable, moist localities generally unfavorable to quadruped life. For example, Shipley (1906.1) observes of the tsetse fly that its

> northern limit corresponds with a line drawn from the Gambia its southern limit is about on a level with the northern limit of Zululand. Most writers agree that the tsetse is not found in the open veldt, that it must have cover. Warm, moist, steamy, hollows, containing water and clothed with forest growth, are the haunts chosen.

This subject will be treated at length under insect life as a factor in extinction.

General effects of decreasing moisture; secular desiccation.—We observe that decreasing moisture (1) changes the character of the food supply by diminishing the softer and more succulent vegetation and increasing the harder and more resistant vegetation; (2) increases the length and severity of the dry season; (3) removes forest barriers and admits new competitors; (4) eliminates animals incapable of traveling long distances for food and water, or living on a limited or irregular water supply; (5) favors grazing quadrupeds and eliminates browsing and forest-living quadrupeds; (6) favors hypsodont (long-toothed) and is inimical to brachyodont (short-toothed) quadrupeds; (7) favors cursorial (rapid-moving) and is inimical to mediportal (slow-moving) quadrupeds.

Secular desiccation (Hann, 1903.1, p. 375) of certain very extensive regions has occurred in parts of all the great continents—North America, Australia, Asia, and Africa—and on each continent we observe a general concomitant modification and extinction of certain kinds of quadrupeds. In general, there appears to have been a progressive decrease of moisture in the Northern Hemisphere, beginning in Oligocene time, which was checked only by the humidity of preglacial time. Increasingly prolonged summer droughts were characteristic of the late Miocene and Pliocene of Europe, and we are beginning to accumulate evidence that the same conditions prevailed in North America.

The great regions of the world where decreasing moisture has introduced a series of changes ending in the extinction of a great number of quadrupeds are (1) North America (Western Plains region, Interior Basin, arid Plateau and Mountain region), beginning in Oligocene time; (2) South America (Patagonia and Pampean region), beginning in late Pliocene time; (3) north-central Africa (the Fayum district), beginning in Oligocene time; (4) central Australia, beginning in Pleistocene time.

American paleontologists, also Stirling (Australia), Andrews (Fayum), and Ameghino (Patagonia), describe faunas adapted to much moister and more hospitable conditions than those which now prevail in the regions they consider.

Sandstorms.—Bravard, who did much to explore the Pleistocene fauna of South America, concurring with Lyell, argued that the great South American mammals were overwhelmed alive by moving sand, as the simoom is said to overwhelm creatures in the Sahara. He invoked for the purpose an exaggerated form of the hurricane, still known in South America as the pampero, and urged that, having been thus killed, they were afterward covered by the sand. Against this hypothesis Burmeister observes that the greater number of the remains that are found are isolated skeletons, most of which, curiously enough, are without heads or tails. Such mutilations do not sustain the idea that the creatures were overwhelmed alive by moving sand.

Secular desiccation and vegetation.—The indirect influences of dry secular changes of climate on quadrupeds are apparently quite as effective factors in extinction as the direct influences, such as changes in vegetation due to decrease of moisture, which make certain types of quadrupeds that were perfectly adapted to one kind of plant food largely or wholly inadapted to the new or altered kinds of food.

Influence of droughts in central Africa.—The influence of the gradual decrease of moisture in a country is clearly illustrated in the conditions which prevail in the African Continent to-day, as observed by Gregory, Foa, and Schillings. Thirst, like hunger, first drives quadrupeds to take extreme risks, which they would absolutely avoid during natural conditions. The drinking places or water pools during long seasons of drought become fewer in number and more widely separated, and large animals driven to them by thirst are more readily attacked and killed by Carnivora. The pools become separated by distances of 30 or 40 miles, thus necessitating long excursions to and from the feeding places, during which the quadrupeds are exposed to attack. Finally some of the pools dry up entirely and, as J. W. Gregory observes (1896.1, p. 268): "Here and there around a water hole we found acres of ground white with the bones of rhinoceroses and zebra, gazelle and antelope, jackal and hyena, * * * all the bones were there fresh and ungnawed." These animals, which had not migrated, had "crowded around the dwindling pools and fought for the last drops of water." Such perishing of animals in great numbers from thirst would bring about diminished herds, spoken of above as the final cause of extinction through inability to protect the young.

Pleistocene desiccation of northern Africa.—There are archeological and even historical proofs (Herodotus) that the central Sahara was once by no means the desert it is now. North of the Sahara—that is, along the Mediterranean coast of Africa—there is evidence of profound changes in climate during and since Pleistocene time. In Pleistocene time this region was still distinctively a part of the African or Ethiopian region. After upper Pliocene time this region enjoyed a warm temperate climate characterized by abruptly alternating dry and rainy seasons; there is evidence of periods of excessive rainfall at the beginning of the Pleistocene epoch. Various indications point to increasingly long periods of drought and progressive secular desiccation of this great region as the Pleistocene advanced, resulting in the partial extinction and partial migration of the great equatorial quadruped life to central and southern Africa (Pomel, 1895.1). Thus the elephants, rhinoceroses, hippopotami, and giraffes disappeared. A typical African fauna was replaced by an equally typical European fauna, which included the bear and the deer.

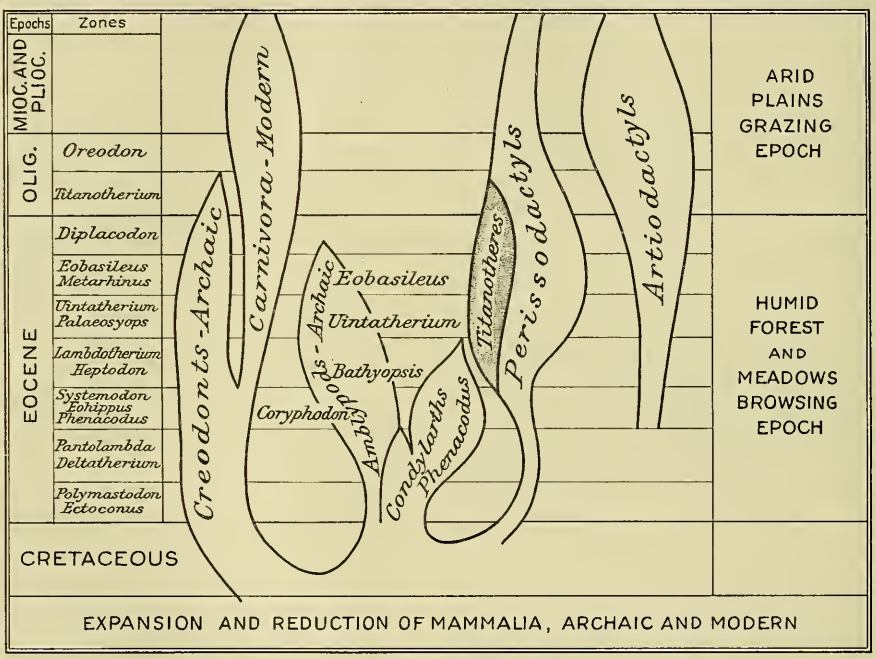

FIGURE 759.—Influence of secular desiccation on the archaic and modern orders of mammals

Desiccation and extinction in central Australia.—Wallace's opinions as to the causes of the extinction of animals in Australia have been cited more as to the effect of the conditions during the glacial epoch and to continental contraction in general than as to the special causes of extinction in Australia. More recent research, set forth by the geologist Tate (1889.1) and the zoologists Hedley (1894.1) and Baldwin Spencer (1896.1), shows that in Pliocene time heavy rainfall or

pluvial conditions, great inland seas or fresh-water lakes (first surmised by Stuart) favored the development of large marsupials. Conversely the rise of an eastern coastal range was followed by diminished rain supply and progressive desiccation of the interior region.

Spencer observes (1896.1, p. 183):

> The larger forms now extinct, such as species of *Diprotodon, Nototherium, Phascolonus, Macropus, Protemnodon*, etc., reached their greatest development in Pliocene time and were characteristic of the eastern interior, spreading southward round the western end of the Dividing Range into Victoria. They do not seem to have reached the eastern coastal district. * * * In post-Phocene time, with the increasing desiccation of the whole central area, they became extinct, though this extinction can not be attributed wholly to the drying up of the land, because in certain parts, such as western Victoria, to which they reached, the state of desiccation did not supervene; but at the same time it may perhaps be justly argued that the desiccation of the vast area of the interior was the largest factor in their extinction.

The discovery (in 1892) of the great Lake Callabona bone deposit in the interior of South Australia abundantly confirms the "desiccation" theory. Dr. E. C. Stirling (1899.1, pp. ii–iii) describes this remarkable deposit as follows:

> There is, however, compensation for the unpromising physical features of Lake Callabona in the fact that its bed proves to be a veritable necropolis of gigantic extinct marsupials and birds which have apparently died where they lie, literally in hundreds. The facts that the bones of individuals are often unbroken, close together, and frequently in their proper relative positions (vide pl. A, fig. 3), the attitude of many of the bodies, and the character of the matrix in which they are embedded negative any theory that they have been carried thither by floods. The probability is, rather, that they met their death by being entombed in the effort to reach food or water, just as even now happens in dry seasons to hundreds of cattle which, exhausted by thirst and starvation, are unable to extricate themselves from the boggy places that they have entered in pursuit either of water or of the little green herbage due to its presence. The accumulation of so many bodies in one locality points to the fact of their assemblage around one of the last remaining oases in the region of desiccation which succeeded an antecedent condition of plenteous rains and abundant waters. An identical explanation has been suggested by Mr. Daintree (1872.1) in his "Notes on the geology of the colony of Queensland."

Alkali and salt deposits.—One effect of increasing desiccation is the increased number of alkali lakes, licks, and springs, and other localities of salt deposits. Alkali is much sought by certain wild animals as a substitute for salt. Western stockraisers disagree as to the effects of alkali upon sheep and cattle, some believing that it can not take the place of salt. Chesnut (1901.1, p. 20) notes that alkali may possibly predispose to the "loco habit," the eating of a narcotic weed. When domesticated animals are not salted regularly they soon discover localities where large quantities of alkali are found in the soil and visit such places frequently for the purpose of eating this alkali soil. (Op. cit., p. 87.)

THE LIVING ENVIRONMENT

PLANTS

We have thus considered the relations of cold, heat, moisture, and desiccation to the hunger, the thirst, and the feeding and the migrating habits of animals. We may now look at the food supply of the Herbivora, especially in its relation to unusual conditions of life.

Forestation, deforestation, and reforestation.—Forests furnish a condition necessary to the existence of certain quadrupeds, especially the browsing animals, such as the Cervidae, which have brachyodont (short-crowned) teeth, and the Proboscidea, including especially the brachyodont mastodon. Among Artiodactyla the deer, among Perissodactyla the tapirs, among Proboscidea the mastodons are typical forest animals. Conditions, therefore, which cause deforestation would become a means of extinction; such conditions are (*a*) intense cold and heavy snow capping, (*b*) intense dryness, (*c*) destruction of young trees by the smaller browsing animals.

It is probable that the interior of Australia and the Pampean region of South America were in Pliocene and early Pleistocene time partly covered with forests. It is certain that the Holarctic region (the circumpolar belt) was forested in early Pleistocene time. Our western arid region was extensively forested at one period. Several of the smaller islands of the Mediterranean have been deforested. Reforestation would confine and limit the desert and plains types. Progressive moisture and reforestation would be very unfavorable to the horse. (Morris, 1895.1, p. 261.) Thus both migration barriers and migration tracts are formed by forests.

Woldrich (1882.1), in considering the glacial epoch, separates into two subclasses the remains of the Quaternary forest fauna of northern Europe, one living entirely in the forests and the other in the intermediate zone between trees and grass. The former comprised *Alces palmatus, Cervus elaphus, C. capreolus, Rangifer tarandus, Bos, Sus, Castor, Sciurus, Myoxus, Arvicola glareolus, Mus sylvaticus, Tetrao urogallus, T. tetrix*, etc. The other and intermediate class consisted of *Rhinoceros antiquitatis, Elephas primigenius, Hippopotamus* (in certain districts), *Bison priscus, Bos primigenius, Megaceros, Rangifer tarandus, Equus fossilis*, etc. All these animals frequent woods; in fact, their daily need of food compels them to live for the most part of the time in forests. The very abundance of their remains proves how luxuriant the contemporary forests must have been, a fact supported by the presence of large quantities of the remains of the capercailzie, essentially a forest-loving grouse, in the caves of Belgium, Yorkshire, etc.

Torrell (1876.1), a Swedish geologist, has argued that it was largely the destruction of the forests in Denmark and Scania which during Neolithic (late Pleistocene)

time extinguished the bison, the elk, the boar, the capercailzie, and the tortoise (*Emys lutaria*).

Poisonous plants.—Domesticated Herbivora generally but not invariably learn to avoid poisonous plants or become more or less immune to their deleterious effects. Generally they are driven by hunger to eat poisonous plants, but there are some exceptions to this rule.

The theory that deleterious or poisonous plants are resorted to by animals under unusual conditions of life is still to be considered among the possible causes of extinction of wild animals. Poisonous plants are widely distributed. Under the unnatural conditions of extreme cold, drought, enforced migration, starvation, etc., they may have influenced extinction, especially on diminished herds.

Chesnut's observations on plant poisoning among the domesticated animals are summarized in a letter written by him to the author (July 9, 1902):

> So far as my observations have extended the chief circumstance leading to death from poisonous plants is an irregularity of the food supply caused by more or less unusual conditions. It does not seem reasonable to suppose that wild animals are frequently poisoned in their native grazing grounds. Sudden disasters, however, might drive them from their feeding grounds into pastures quite unfamiliar to them, where they would undoubtedly be more or less at a loss to distinguish between poisonous and nonpoisonous plants.

Hornaday, on the other hand, in a letter written to the author in 1906, observes:

> There appears to be no evidence that any wild herbivorous species ever has been seriously affected by eating poisonous plants. All the cases cited by Chesnut and other authors under this head are domestic species only. Tame species have, through man's care for their wants, lost the discriminating instinct which protects the wild species. For example, the antelope, buffalo, elk, and mule deer never eat loco weed on the southern plains; the deer of the Appalachian region do not eat the leaves of the laurel, which are so fatal to the domestic goat.

Beebe in a letter to the author dated January 17, 1912, observes:

> Darwin was in error when he stated [67] that "The root of the *Aconitum napellus* becomes innocuous in frigid climates." Hooker was also wrong when in the "Flora of British India" he lumped a number of distinct species under the name *Aconitum napellus*, which, as a fact, does not occur in British India. The poisonous aconite of Sikhim is *A. ferox*. In Nepal four varieties of *A. napellus* are found, two of which (*A. napellus* and *A. rigidum*) are poisonous and two (*A. multifidium* and *rotundifolium*) are eaten by Bhutian hill men, and also by the Impeyan pheasant (*Lophophorus*) and panda (*Aelurus*). The domestic sheep can not distinguish between the poisonous and nonpoisonous forms (sheep are protected by muzzling); the wild creatures can distinguish.

Wild animals are certainly protected, both by instinct and by experience, from poisoning by plants. This fact, however, does not exclude the possibility that, under certain harsh or unusual conditions of life, deleterious or poisonous plants may have hastened a diminution of their number. There may also have been occasions when such plants constituted a new and unfamiliar danger. Some molds and smuts that appear on the Gramineae are periodic, not constant; under changing geographic conditions certain narcotic plants may have been introduced and spread rather suddenly; ergot, a morbid growth arising from a diseased condition of the ovary of various grasses, produced by a fungus of the genus *Claviceps*, may cause diseases of the hoof. We must also consider the effect of the introduction of certain poisonous plants that do not injure the parent but may injuriously affect or kill the suckling young. The distribution of most of these plants is related to increase or diminution of rainfall.

There are also marked variations in the degree of immunity. Linnaeus, in his "Tour in Scania," as cited by Lyell (1872.1, p. 440), tells us that goats were turned into an island that abounded with *Agrostis arundinacea*, which they would not eat, so that they perished by famine, but that horses which followed them grew fat on the plant. The goat, he also says, thrives on meadow sweet and water hemlock, plants that are injurious to cattle. Observations in South Africa (Hutcheon, 1906.1) give similar results. The "chinkerinchee" plant (*Ornithogalum*) is poisonous to horses, and one of the ragworts (*Senecio*) is an irritant causing cirrhosis of the liver in cattle and horses. Tulps (species of *Moraea*) also give trouble. Most of the cattle thus lost are not accustomed to the country or are very hungry trek cattle.

Fatal effects of wet seasons.—Chesnut (1901.1, p. 19) observes that most of the plants that are especially poisonous during the wet season are so much shriveled in the dry season as to be absolutely unpalatable. Sheep owners have accordingly found that mountain ranges whose growths are extremely dangerous for sheep during the wet season of early summer are quite safe from July to September, inclusive. Similarly, during the wet season and when feeding immediately after heavy rainstorms domesticated animals are more likely to pull up the roots of plants than when the ground is dry, and (idem, p. 26) in many poisonous plants it is chiefly the roots that contain the poison.

Snowstorms as affecting eating of poisonous plants.—After heavy snowstorms, when the grass is covered by snow, it often happens that only the taller species of plants are exposed (idem, p. 27). At such times the poisonous larkspurs (*Delphinium glaucum*) are greedily eaten by cattle, which at other times avoid these plants. This danger is increased by the fact that ruminants do not feel at ease so long as their stomachs are not full, and they are inclined to eat anything in sight after a snowfall. In seasons of drought certain poisonous leguminous plants remain green and tempting after the grasses have become

[67] Animals and plants under domestication, Westminster ed., II p. 255.

thoroughly dried. Cattle on the range then take the loco and lupine (idem, p. 29).

Enforced migration and poisonous plants.—Chesnut observes (idem, p. 21) that domesticated animals when feeding quietly on the range exercise considerable choice in selecting forage plants, but that when they are being driven 6 or 8 miles a day they may be forced by hunger to bite off almost all kinds of plants that grow along the course of their travel. Enforced migration among wild animals might similarly cause them to become less fastidious about food.

Distribution of poisonous plants.—The chief poisonous plants of the Montana stock ranges (Chesnut, 1901.1) are the death camass (*Zygadenus*), favored by moderate moisture and taken by sheep; the "tall larkspur" (*Delphinium glaucum*), favored by moderate moisture, taken by cattle; the "purple larkspur" (*D. bicolor*), taken by sheep; the water hemlock (*Cicuta*), found along watercourses, taken by cattle and sheep; the white loco (*Aragallus*), taken by horses, sheep, and cattle. Lupines (*Lupinus*) in certain stages of growth are poisonous to sheep. Ergot (*Claviceps purpurea*) occurs in Montana on a variety of grasses and is occasionally poisonous to horses and cattle, producing a disease of the limbs. On a large ranch of Wyoming, according to Walter Granger (letter, 1904), ergot appeared as a result of irrigation, rendering a large tract fatal to horses and cattle by causing a disease of the hoofs.

A leguminous plant of Egypt (*Lotus arabicus*), recently investigated by Dunstan and Henry, as a growing plant is poisonous to horses, sheep, and goats. It contains a glucecoid termed "lotusin," which is poisonous when taken into the stomach (Chesnut, 1902.1, p. 1019). Its seeds when ripe, however, are commonly used as fodder.

Narcotic plants.—Among narcotic plants "loco weeds" are the most interesting as one of the possible causes of the extinction of wild animals. "Loco," a Spanish word meaning mad or crazy, is applied in northern Mexico and the southern United States to certain plants which so affect the brain of animals as to give them all the symptoms of brain disease. As described in the important paper of Chesnut (1899.1, pp. 403, 404) the weeds called "loco" belong to genera of the pea family. He writes (1902.1, pp. 87–90):

> For many years a disease called loco, affecting cattle, horses, and sheep, has been generally known to the stockmen of the western ranges. This disease has most commonly been attributed to the action of certain plants, more rarely to that of alkali. Several species of plants have been suspected of producing the loco condition in animals and have been called loco plants or loco weeds and also crazy weeds, from the nature of the disease. Nearly all of the plants which have been considered loco weeds belong to two genera of the pea family, *Astragalus* and *Aragallus*. These genera are represented by numerous species on the western stock ranges. * * * From a general description given of the loco disease it is apparent that this condition might very justly be termed a perverted appetite. * * * The horse and the sheep are the animals which are most frequently affected by loco disease. Cattle occasionally acquire the loco habit, but the cases are comparatively rare. In certain parts of Montana the habit became so widespread among horses that the raising of them was abandoned until the locoed animals were disposed of and other horses which had not the loco habit had been imported. * * * During the progress of field work in Montana in 1900 about 650 locoed sheep and 150 locoed horses were seen.

Mechanically dangerous plants.—Occasional losses of stock occur in Montana from plants acting mechanically. For example, the sharp-barbed awns of the porcupine grass (*Stipa spartea*) and squirrel tail (*Hordeum jubatum*) when the plants are maturing separate and, entering the mouth, throat, eyes, and ears of stock, affect the tissues and give rise to ulcers which cause intense suffering and necessitate killing. (Chesnut, 1902.1, pp. 50–51.) Similarly the cornstalk disease is sometimes attributed to malnutrition or impaction of the alimentary canal.

In this connection may be cited an observation recorded by Thiselton-Dyer (1902.1), which happens to bear upon the life of goats:

> The introduction of the sweetbrier into New South Wales, Australia, in many parts of which it is naturalized, affords a striking illustration of the mode in which the balance of nature may be disturbed in a wholly unforeseen way. * * * The fruit of the sweetbrier (*Rosa rubiginosa*) consists of a fleshy receptacle lined with silky hairs, which contains the seedlike carpels. * * * The hairy linings of the fruit caused the death of a number of goats by forming hairy calculi, which mechanically occluded the lumen of the bowels. These goats were put on the land with the idea that they would eat down the briers and ultimately eradicate them, but the briers came out best and eradicated the goats. The cattle running on the land are also very fond of the brier berries, and from time to time one will die, and on post-mortem [examination] no pathological changes can be found in any of the organs, nor do the hairy calculi appear in them, although their various stomachs are one mass of the brier seeds.

INSECTS AND PROTOZOA

The main features of physical environment, such as moisture and desiccation, heat and cold, can not be considered by themselves or solely in relation to the plant life; they must be studied also in relation to the insect life which they condition. Insect and parasitic life is now known to be one of the greatest factors in the numerical reduction and probably therefore in the extermination of mammals. Greater progress has been made in this study than in any other since Darwin's time, yet Lyell and Darwin both adumbrated the modern discoveries.

Insects and the food supply.—The periodic devastations of certain insects, especially those caused by locusts as cited by Lyell, in Europe, Arabia, India, and northern Africa, are sufficient to cause the reduction of certain species. As Lyell concludes (1872.1, vol. 2, p. 445):

> The occurrence of such events at certain intervals, in hot countries, like the severe winters and damp summers returning after a series of years in the Temperate Zone, may effect the

proportional numbers of almost all classes of animals and plants and probably prove fatal to the existence of many which would otherwise thrive there; while, on the contrary, the same occurrences can scarcely fail to be favorable to certain species which, if deprived of such aid, might not maintain their ground.

Insect barriers.—We may first consider the influence of the introduction into habitual feeding grounds of various forms of insect life which render these grounds practically uninhabitable and either kill or drive the animals out. Thus Darwin, as quoted by Wallace (1889.1, p. 19), observes:

> In several parts of the world insects determine the existence of cattle. Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater numbers, in Paraguay, of a certain fly which lays its eggs in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by other parasitic insects. Hence, if certain insectivorous birds were to decrease in Paraguay, the parasitic insects would probably increase; and this would lessen the number of the navel-frequenting flies; then cattle and horses would become feral, and this would greatly alter (as indeed I have observed in parts of South America) the vegetation; this again would largely affect the insects, and this, as we have just seen in Staffordshire, the insectivorous birds, and so onward in ever-increasing circles of complexity.

Insects and infection.—As noted above, the most striking advance toward a complete theory of natural extinction has come from recent discoveries regarding the real nature of animal diseases and how they are communicated. Only recently have we come thoroughly to realize, first, that insects are the most active means of introducing and spreading fatal diseases over great geographic areas and on a vast scale; second, that certain immune mammals become the bearers and disseminators of these diseases.

Aflalo in his paper "The beasts that perish"[68] has discussed many of the various causes of extermination and gives disease a prominent place. Among the Carnivora there are the nonepidemic diseases, such as distemper, affecting dogs, foxes, wolves, cats, and other wild felines. The more rare and sporadic epidemics claim victims among the Carnivora wholesale. The prevalence of rabies among foxes was observed on the continent from 1830 to 1838 in Switzerland, also in Württemberg and Baden.

Ticks in Africa.—Roosevelt (1910.1) dwells on the extent to which African wild mammals are persecuted and infested with ticks, to which, however, they seem to have become so habituated that they dread them much less than the biting flies; the ticks, even where they do not introduce disease germs, are very weakening as bloodsuckers. Many birds devote themselves to little else than the picking off and eating of the ticks and fleas infesting the mammals; if these birds were killed off the mammals would suffer far more.

[68] The original article has not been accessible to the author.

Johnston notes (1910.1) that certain types of heron (egret) are perpetually snapping at tsetse and other flies which settle on oxen or game and probably destroy a considerable proportion of these disease-carrying insects.

Ticks as rapid spreaders of disease among domestic ruminants.—*Piroplasma parvum* is a protozoan which, unlike the trypanosome, invades the blood corpuscle. It is malignant with cattle along the greater part of the east coast of Africa, causing what is known as east-coast fever. The infection is usually transmitted by ticks, most frequently by the brown tick, *Rhipicephalus appendiculatus*, also by *R.* (*Cerotherium*) *simus*. Migrating or trekking cattle may carry the ticks many miles a day and thus spread the disease rapidly over a wide area. The larva creeps on an infected animal, sucks some of its blood, drops off, lies among the roots of the grass, and passes its first molt, becoming a nympha, then an imago, in either of which stages it may infect a healthy animal by creeping from the grass. The tick is very hardy and may survive with its infection for a year, but after a year or 15 months the infected ticks are all dead, so that healthy cattle may reenter the field without risk. It takes two years to starve the ticks out of a country by removing the cattle. This method was employed in the Wichita National Bison Preserve, the bison (*Bison americanus*) being very susceptible to "red-water fever." If this tick had been introduced centuries ago among the bison it might have exterminated them.

Wide geographic distribution.—The geographic distribution of the species of *Piroplasma* is very wide; first discovered in North America, it is now epidemic throughout most of South Africa. *Piroplasma bigeminum* similarly causes the "Texas" or "red-water" fever of our Southern States. It is conveyed by a tick. The germs are latent, and the blood of an animal that has recovered from Texas fever remains infective. Thus apparently healthy cattle may infect imported susceptible cattle. Such latency has a significant bearing upon the theory that natural extinction may be caused by similar germs. Although they acquire immunity, the domesticated native Bovidae act as reservoirs of the disease, in contrast to the tsetse-fly disease, in which the wild Bovidae act as reservoirs. The further fact that native cattle may become immune has an important theoretical bearing on the natural origin of immunity to the tsetse-fly and other diseases among the wild Bovidae and wild Equidae.

Ticks among Equidae.—The biliary fever of domesticated Equidae (horses, mules, donkeys) is conveyed by a corpuscle parasite (*Piroplasma equi*), which is spread by the red tick (*Rhipicephalus evertsi*), the infection being taken in the nymphal and transferred in the adult stage. The native South African horses, like cattle that are exposed to Texas fever, become

immune to the disease and are said to be "salted," but horses that have recovered from the disease continue to act as reservoirs and remain sources of infection throughout their lives.

The same is true of *Piroplasma canis* among the Carnivora spread by the dog tick (*Haemophysalis leachii*). The blood of recovered animals remains infective.

EPIDEMICS

Epidemics in North America.—We are indebted to Thompson Seton (1909.1) for bringing together a large number of observations recorded by many authors on epidemics among the American mammals. In the summer of 1873 a fatal epidemic is said to have destroyed three-fourths to nine-tenths of the prong-horn antelopes (*Antilocapra*) in the area between Yellowstone and Missouri Rivers in Montana (Allen). An epizootic distemper called black tongue killed thousands of white-tailed deer in Texas in 1856 (Walton). Tuberculosis broke out among the New England deer in 1901, destroying chiefly the older ones (Murch). A species of distemper killed off vast numbers of the beaver of upper Red Deer River, Alberta, about the year 1800, and they have never been so plentiful in that region and eastward to Hudson Bay since that year (Tanner). In western Manitoba the wonderful "rabbit year," 1886, in which these animals are said to have multiplied to the number of 5,000 to the square mile, was followed in the ensuing winter by a destructive plague due to a staphylococcus which may have started in some skin wound or parasitic skin disease (Little); from a condition of extraordinary abundance the rabbits practically disappeared. According to Hornaday a parasite, the bloodsucking stomach worm (*Strongylus strigosus*), may have caused the so-called seven-year plague among northern varying hares (*Lepus variabilis*) and the rabbits of the West. Seton observes that the great periodic decrease in the lynx, which in every 10 years or so reduces their number to about one-tenth of the maximum, is probably due indirectly to the periodic rabbit plagues—that is, to starvation through failure of the rabbit supply. Many emaciated bodies of the lynx are found in such seasons.

Epidemics in Europe.—Fleming, in his "Animal plagues" (1871.1), enumerates eighty-six epidemics that affect wild quadrupeds and birds. In the list are diseases that affect nearly every wild species in Europe and some in the New World, including the red deer (*Cervus elaphus*), the reindeer (*Rangifer tarandus*), the chamois (*Rupicapra tragus*), and the wild hog; also, among the Carnivora, wolves, foxes, and bears; among the Rodentia, hares, rabbits, and rats. Various forms of tuberculosis account for a large percentage of death among domesticated animals. Among animal plagues anthrax was formerly the most rapid and deadly, but it is now perhaps the least common, owing to Pasteur's discoveries. American zoologists are familiar with the spread of disease from domesticated to nondomesticated animals—of the sheep scab, for instance, to the wild sheep (*Ovis montana*).

The feline and ursine Carnivora are protected by their relatively nongregarious habits; canids are highly gregarious and consequently would be more subject to the spread of eipdemics. On the contrary, the gregarious Herbivora offer favorable conditions for the spread of disease.

Epidemics in Africa.—In his "Great Rift Valley" Gregory (1896.1, pp. 265–266) observes that the great herds of game which roamed over the steppes of South Africa are being rapidly decreased. Man no doubt has played the leading part in the annihilation of the enormous herds that once thronged Cape Colony. The fact that during the last few years the game has retreated from the Somali coast into the interior shows how easily it can be driven from a district. In South Africa, however, man's work of extermination has probably been insignificant as compared with that of natural agencies, such as lions and disease. Vast herds of the wild buffalo (*Bubalus caffer*) were exterminated between 1890 and 1893 by the cattle disease (rinderpest), which also killed off the gnu and giraffe. Cumming (1855.1, vol. 1, p. 138) observed as early as 1855 that

> the goat in many districts is subject to a disease called by the Boers "brunt sickta," or burnt sickness, owing to the animals afflicted with it exhibiting the appearance of having been burnt. It is incurable, and if the animals afflicted are not speedily killed, or put out of the way, the contagion rapidly spreads, and it is not uncommon for a farmer to lose his entire flock with it. This sad distemper also extends itself to the ferae naturae. I have shot hartebeests, black wildebeests, blesbucks, and springbucks, with their bodies covered with this disease. I have known seasons when the three latter animals were so generally affected by it that the vast plains throughout which they are found were covered with hundreds of skulls and skeletons of those that had died therefrom.

Howorth observes (1887.1, p. 174):

> Frequenters of the forest with whom I have conversed, whether Europeans or Singhalese, are consistent in their assurances that they have never found the remains of an elephant which had died a natural death. One chief, the Wannyah of the Trincomalee district, told a friend of mine that once after a severe murrain, which had swept the province, he found the carcasses of elephants that had died of disease.

Entozoa in elephants.—Several specimens of the African elephant (*Loxodon africanus* Blumenbach) were autopsied by MacCallum (1907.1). Little has been written about the Entozoa of this species, which apparently differ in many respects from the better-known forms infecting *Elephas indicus*.

It is said that elephants succumb to the infestation of parasites more than from any other cause, and the worm that most often destroys these animals is a species of *Paramphistomum*. Members of this genus

of trematodes are commonly parasitic among the Herbivora in tropical countries. They infest the stomach and intestines in great numbers and not only deplete the animal's energy by exacting a great quantity of blood but disturb the lining membrane of the stomach and intestine so as to interfere seriously with the secretions and digestion. Several species of worms may be found in the same region.

When it is suffering from the attacks of these parasites the elephant is said to make instinctively an attempt to get rid of them by eating 10 to 20 pounds of a certain red earth, which acts as a purgative, dislodging and expelling a lot of worms. In India, where there are domesticated herds of 400 or 500 of these valuable animals, the loss from Entozoa is sometimes serious.

Parasites in air sinuses.—Larvae that invade the frontal sinus of the skull are among the possible causes of the extermination of animals. An old trapper and close observer in British Columbia, Mr. Charles Smith, informs the author that both the wild sheep of the region (*Ovis montana*) and the wapiti (*Cervus canadensis*) are seriously affected or killed by inflammation caused by these larvae. The overcrowded caribou of Labrador and Newfoundland suffer from a fly which lays its eggs in the nasal passages.

Allen (1906.1, p. 201) states that there is a pathologic modification in the skulls of peccaries (*Tayassu*), due to parasites lodging in the orbitosphenoid and adjacent parts. He observes:

> In this connection an examination has been made of nearly 50 skulls of peccaries, in the [American] Museum collection from various parts of South America, with the following results: In a series of 17 skulls of *T. pecari* from Santa Marta district of Colombia, all were found diseased in the manner above described, so that this condition might readily be mistaken for the normal. In 20 skulls of *T. torvum* about 80 per cent show the diseased condition strongly, and others show traces. Of 9 skulls of *T. tajacu* from Chapada, Matto Grosso, Brazil, 2 only are normal. The inflation of the bones forming the antero-inferior wall of the orbit, through the invasion of these parts by some parasite, is so general in the whole group of peccaries that the absence of such conditions seems to be almost exceptional.

Moisture favoring the spread of diseases carried by insects.—The presence of the blood protozoan parasites known as trypanosomes, combined with certain flies which act as disease carriers, is in many countries correlated with wet weather. This is especially true of the disease known in India as "surra," the history of which was first suspected by Surgeon Major Lewis in 1888 (1888.1). In South America the mal de caderas affects horses, asses, cattle, hogs, and certain other animals and is attributed to the protozoan known as *Trypanosoma equinum*. It is distinctively a wet-weather disease, almost completely disappearing in dry seasons. Asses, swine, and water hogs are said to be affected, and horses are never known to recover. It is chronic in course, lasting from two to five months in horses and from six to twelve in asses and mules. See Voges (1902.1) for fuller details.

Extermination of the Equidae.—The wide geographic range of surra and related diseases is significant with reference to former periods in the history of the Equidae. All authors now agree with Lewis that the disease is carried by flies and coincides with wet weather, occurring chiefly during or immediately after heavy rainfall, though sporadic cases may occur at other seasons of the year. In the "Emergency report on surra" by D. E. Salmon, C. W. Stiles, and A. Hassall (1902.1, p. 18), this is described as chiefly a wet-weather disease, invariably fatal to horses and mules, occurring in other animals, such as camels and elephants, more rarely in ruminants, and transmissible to goats, sheep, and other mammals. In India it is said to affect horses, camels, and elephants. It occurs in Burma, Persia, Tonkin, and Chosen. In Africa there is the similar nagana, or tsetse-fly disease, more accurately described by Bruce (1905.1, p. 333). In Algiers, France, and Spain the dourine or maladie de coit attacks the horse and ass in particular and may be transmitted to certain other animals. It is attributed to a trypanosome, *T. equiperdum*. In the Philippines surra caused the death of 2,000 army horses in six months. The intermediary is a fly, *Stomoxys calcitrans*. It was also reported (Curry, 1902.1) as affecting the carabao, *Bos* (*Bubalus*) *kerabau*, but according to Lingard ruminants are not particularly susceptible.

An interesting bit of advice given to those in charge of horses in the Philippines may have some bearing upon the origin of colors in certain quadrupeds: "Avoid light-colored animals as much as possible; the darker the animal the safer he appears to be from the attack of flies." In this connection we recall the dark color of the true Bovinae, the wild cattle.

Tsetse-fly disease of domesticated Equidae and Bovidae.—The nagana or tsetse-fly disease of Africa is caused by *Trypanosoma brucei* (Plimmer and Bradford, 1899.1; 1902.1); the carrier is the tsetse fly (*Glossina morsitans*). Together this trypanosome and its host, the fly, render thousands of square miles of Africa uninhabitable; no horses, dogs, or cattle can venture even for a day into the "fly country." After all the nonimmune animals of the country have been killed off and thus there no longer exist sources of infection, the tsetse fly spreads abroad out of the "fly country," still giving rise to the disease. This strange fact led to the discovery of the fact noted above—that many of the immune wild ruminants carry the same trypanosome (*T. brucei*) in small numbers in their blood and thus act as continuous reservoirs of the infection; it is from them that the fly receives fresh supplies of the infectious parasite. A similar

parasite also lives in the blood of healthy rats. Analogous to this is the "sleeping sickness" that affects man, which has spread rapidly from west to east Africa, carried by a fly, *Glossina palpalis*, claiming hundreds of thousands of victims.

Rinderpest in Africa.—The rinderpest or cattle disease has been the greatest destroyer of the wild African quadrupeds. This disease has been known from time immemorial in Europe and central Asia. It is believed by some to have entered the Nile provinces of Africa in 1880, to have reached the Transvaal in 1896, and thus to have traveled the whole length of the Dark Continent. It has been spread largely through the infection of wild ruminants. It is fatal to the wild buffalo, *Bos* (*Bubalus*), the kudu (*Strepsiceros kudu*), the sable antelope (*Hippotragus niger*), the gnu (*Connochaetes albojubatus* and *C. taurina*), also in the Philippines to the carabao, *Bos* (*Bubalus*) *kerabau*. It is fatal to 90 to 100 per cent of domesticated cattle. The parasite causing rinderpest is undiscovered, no natural immunity is known (methods of artificial immunity were discovered in 1893), and it is distinguished by the ease and rapidity with which it spreads in all countries, climates, and seasons, being carried even on the clothes and person of man. It therefore appears improbable (Bruce, 1905.1) that insects have anything to do with it. It may be due to a wind-borne bacterial organism.

By analogy we may imagine that a disease affecting the Pleistocene horses of North America may have traveled an equal distance, from Texas to Patagonia, and destroyed all the South American Equidae.

Moist rhinarium and other eliminating causes in Africa.—The rinderpest of 1889–1899 illustrated the eliminating value of a single organ, the external nostril. Rinderpest (see above) is fatal to domestic cattle, to all the Bovinae and to the antelopes most closely approximating to them, including the tragelaphines (eland, kudu, bushbuck, reedbuck, dyker), all these ruminants having a large, moist rhinarium, whereas animals with a small, part hairy rhinarium—the sable antelope, roan antelope, hartebeest, impala—suffered much less if at all.

The wildebeest and hyena, although immune to rinderpest, are hosts of the nagana trypanosomes, which are carried by the tsetse fly. In the region of the middle Zambezi the buffalo perished in enormous numbers, the remains of 200 animals being observed within a few acres—piles of bones and skulls, a veritable Golgotha. Geographically the course of the rinderpest was most erratic, here diverted by a range of mountains, there sweeping down one bank of a river and leaving the other untouched. Subsequent to the rinderpest epidemic the tsetse fly was eliminated over certain areas, especially those that had been covered by the rinderpest south of the Zambezi. Whether the elimination of the fly was in any way connected with the rinderpest is a matter of speculation.

As a result of the rinderpest epidemic in South Africa the last of the elands disappeared and the buffalo were reduced to one herd of about 20. In the Sabi Bush the kudu were greatly thinned down, whereas south of the Zambezi, in British Nyasaland, the rinderpest made no difference whatever in the status of the fly; possibly climatic conditions or some parasitic enemy caused the decrease of the flies.

Pleistocene extinction of horses.—Among all the problems of Pleistocene extinction presented in America that of the horses is certainly one of the most difficult. These animals are far superior to cattle in their adaptability to changing conditions of life and in resourcefulness in severe winters. They were very numerous in North America at the beginning of Pleistocene time, whereas at the end of it they were apparently extinct. Similar extinction occurred both in North and South America at this period. The numerous and highly specialized horses of Mexico shared in this extinction, although we might have regarded the high plateau of Mexico as a ready means of escape from the more severe conditions in the north in the glacial epoch. It has consequently been suggested by Osborn (1906.287) and by others that the American horses may have been swept out of existence by some epidemic disease or diseases. This theory has subsequently received some support through the discovery by Cockerell (1907.1; 1909.1) of two species of fossil tsetse fly (*Glossina*) very similar to the African types of to-day. These flies are found in the Florissant lake beds of Colorado, which are regarded as of upper Miocene age, and were contemporaneous with the varied equine fauna.

Ticks and horses.—Ticks, even those that bear no infection, form effective barriers to the introduction of quadrupeds into certain regions. In some forested parts of South and Central America they endanger human life. In certain regions of Africa ticks are practically fatal to horses. As stated orally by Dr. D. G. Elliot, thousands of ticks may gather on a horse as a result of a single night's grazing. The mane especially serves to collect these pests. Thus the falling mane of the northern horse is distinctly disadvantageous as compared with the upright manes of the asses and zebras. Ticks are capable of driving certain types of animals entirely out of a country and of indirectly causing certain modifications of the hair and epidermis.

In the forests of southern California prickly seeds of certain plants find their way into the nostril sac of horses and cause serious if not fatal abscesses unless removed.

Distribution of horse sickness.—Horse sickness is local in distribution, prevailing in low countries and during wet seasons. The same climatic relation is

true of the heart-water disease of cattle, goats, and sheep (Bovidae), which is similar in distribution to the horse sickness and is carried by the bont tick (*Amblyomma hebraeum*), in that it dies out on the high veldt. The "catarrhal fever" of sheep has a distribution in South Africa similar to that of horse sickness and is probably carried by means of the same night-feeding insect. The infection causing horse sickness is not carried into the high country nor during the dry season; the parasite is unknown and is believed to be ultramicroscopic; it is believed to be carried in the blood, because the one-thousandth part of a single drop of blood injected under the skin of a healthy animal will cause death; some horses require a larger dose than others, indicating fluctuations in power of resistance or immunity. Unlike the foregoing diseases it is not endemic or permanent but occurs in epidemics at intervals of 10 to 20 years. Its geographic distribution in South Africa is very wide, including Natal, Zululand, the greater part of Rhodesia, Bechuanaland, and Portuguese East Africa. Horses placed in fly-proof shelters, even in exceedingly unhealthy places, in no case incur the disease. The particular fly or insect carrier is still unknown. As in several of the foregoing diseases the infective power of the blood persists for years.

Summary as to natural extinction by epidemics.—To summarize these remarkable observations, which we owe to the labors of Lewis, Koch, Theiler, Kilborne, Smith, Watkins-Pitchford, Lounsbury, Salmon, Curtice, Stiles, Hassall, Taylor, and many others, we undoubtedly have an agency that must be considered an occasional if not a frequent cause of the extinction of quadrupeds in the past.

It will be noted (1) that in the case of the tsetse-fly disease the wild ruminants are the permanent though unharmed carriers to domestic animals of the infective protozoan; (2) that, on the contrary, in the Texas fever, or "red-water fever" the native immune Bovidae are the permanent carriers of the disease organism to the wild Bovidae (bison); (3) that the rinderpest now appears to be in an early stage of its history as a disease in which neither domesticated nor wild Bovidae have become naturally immune, and all the Bovidae act as reservoirs; (4) that in the east-coast fever the infective ticks survive for a year and the permanent carriers of the infective organism are not yet discovered; (5) that in the biliary fever of domesticated horses the recovered equines act as reservoirs; (6) similarly again, that in the "horse sickness" of South Africa the infective power of the blood in a recovered animal persists for years.

Thus in these modern cases we have all the theoretical conditions favorable to the wide distribution of insect-borne diseases which in past times may have attacked various types of quadrupeds and resulted in extermination before natural immunity was acquired.

BIRDS

The relation of birds to the life of insects that attack mammals, and thus to the existence of mammals themselves, has already been mentioned. The closest relation of birds to the protection of mammal life is that of destroyers of the insects which infest and infect mammals.

The bird that is most notably destructive to mammals is said to be the kea, the New Zealand parrot (Wallace, 1889.1, p. 75). The sheep-killing habit of the kea has recently been declared mythical. W. B. Benham (1906.1; 1907.1), however, asserts that the kea causes great mortality among the sheep of the high mountainous country of the South Island; in other parts of New Zealand it is absent. The kea perches on the back of the sheep and soon eats a hole into the abdomen. It is not known whether this is for the purpose of getting the blood or of eating the kidney fat, as was formerly supposed. The sheep are often found with a hole so large that the entrails exude and the animal has to be killed. The kea does a great deal of its work at night, and for this reason a great many people have not been able to observe it and have doubted the truth of the statements. Other birds are known to have turned from herbivorous to carnivorous habits.

MAMMALS

Forms of competition.—From consideration of the struggle of animals with their physical environment and with their living plant, insect, and bird environment, we now pass to consideration of the more intimate struggle with other mammals. It is important to note that the struggle in this intermammalian competition is always intensified during periods of geographic, climatic, and biotic change. This struggle naturally presents a variety of phases, such as competition of lower and higher types of mammals, struggle between Herbivora and Carnivora, struggle between Herbivora and Herbivora, competition between resident and newly introduced forms, and competition between less and more adaptive types.

Even in comparison with the supposed climatic, plant, and insect agencies, the competition between lower and higher types, or between less and more adaptive types, or between slowly producing and rapidly producing types has been the chief direct agency of extinction, because it has worked more widely and over longer periods of time.

During the introduction of new types in the Tertiary period in North America, we witness more than once the apparently unchecked multiplication of certain local or native mammals; the repeated introduction or migration of new mammals, either singly or in waves; and the slow or rapid sequent extinction of certain local mammals. These cycles of change may be due to remote geographic conditions but are frequently connected with or sequent upon

independent local physiographic changes. Early theoretic observations on this principle are those of Lyell and Darwin. Lyell observes (1872.1, vol. 2, p. 451):

> Extension of the range of one species alters that of others. In reference to the extinction of species it is important to bear in mind that when any region is stocked with as great a variety of animals and plants as its productive powers will enable it to support, the addition of any new species to the permanent numerical increase of one previously established must always be attended either by the local extermination or the numerical decrease of some others.

Wallace observes: "There is good reason to believe that the most effective agent in the extinction of species is the pressure of other species, whether as enemies or merely as competitors." Darwin entertained similar views.

The evidence afforded by paleontology does not fully support the sweeping statement made by Wallace, for paleontologic research indicates that competition is chiefly between phyla. The conclusion drawn from these exceptions is similar to that of Darwin—that the keenest competitors are animals of most nearly similar feeding habits.

There are, however, exceptions to Darwin's conclusion also, as several examples to be cited demonstrate. The extinction of the titanotheres and elotheres may have been due entirely to changes in vegetation rather than to competition with other Herbivora. Again, the survival of the opossums (didelphids) in North America is a striking instance of successful competition of a very generalized type of marsupial with numerous other small Carnivora by the adoption of nocturnal habits.

Competition between placentals and marsupials.—The gradual introduction of placentals into Australia has recently been summarized by Lucas and Le Souëf (Lucas, A. H. S., 1909.1, p. 4). The rodents probably became denizens of the continent in later Tertiary time. They probably came from Asia, for there are no groups related to the peculiar genera of South America and the Cape. The rodents all belong to the widely distributed family of the Muridae. The most specialized genus is *Conilurus* (*Hapalotis*), comprising graceful little rats, which take the place of the leaping jerboas of Africa and Asia. Then came in the dingo, a wolf from eastern Asia. Lastly, introduced directly from Europe, came a disastrous and prolific population of black and brown rats, the common mouse, the rabbit and the hare, and, worst of all, the fox. During the year 1908 no fewer than 18 million rabbit skins passed through the Sydney market, besides a nearly equal number through the Melbourne market, and vast numbers of rabbits were exported in cold storage, but these inroads produced little effect in exterminating the pest.

Baldwin Spencer observes (1896.1, p. 127) that the existing marsupials are severely handicapped when in competition with the rodents by having to carry their young in the pouch; at the age when a young marsupial at sight of danger at once flies to its mother's pouch, a young rat or rabbit is taking care of itself. If a hawk or eagle catches the mother rabbit the young one is left, or vice versa. The marsupial mother has to carry the young ones, and not only does the extra weight prevent her from gaining shelter, but if caught both she and the young ones are sacrificed. A very slight difference in speed will save or lose an animal's life. When hard pressed a kangaroo will throw the young out of the pouch so as to travel faster. The same author (idem, pp. 55–57) in considering the causes of the extinction of the giant Pleistocene kangaroos attributes it to overdevelopment in size during a humid period followed by strenuous competition of food during an arid period.

Reduction of food supply by smaller Herbivora.—The great changes in the life of the countries encircling the Mediterranean are attributable in part to changes of climate, in part to the destructive agency of man, and in part to the destructive agency of animals introduced and protected by man. The change both in soil and vegetation has been caused indirectly by deforestation of the hills and mountains, and this has been largely due to the unrestricted browsing of large herds of sheep and goats, which has been going on since long before the Christian era. Even now goats may be seen in certain parts of Palestine and Greece destroying the last of the forests by killing the seedling trees. The destruction of the forests leads to the washing away of the soil, unfitting a country to support any of the larger Herbivora. Man has played so large a part in this disturbance of the natural order that it is hazardous to use these illustrations as analogous to natural conditions in the distant past.

The competition of the smaller Herbivora, especially on islands, is one which, although by no means demonstrated, is a possible cause of the extinction of the larger Herbivora in past time. For example, in South Dakota and Nebraska the small browsers, such as the oreodonts and horses, which swarmed in herds in lower Oligocene time, may possibly have affected the food supply of the large titanotheres. In Oligocene Europe, similarly, the great multiplication of the small browsers, known as cenotheres, may have been prejudicial to the larger mammals.

The introduction of new forms of browsing and grazing animals may in certain periods have disturbed the balance of nature and altered the character and amount of food supply and even the water supply and set up new forms of animal competition in certain regions. The placental rabbits to-day certainly exert a great influence on the natural food supply of the marsupial Herbivora of Australia. Cases of overmultiplication are rare in nature, yet not un-

known, as seen in periodic multiplication of the hares in British Columbia cited above. The United States Biological Survey has recorded the startling total of 10,000 to 12,000 field mice to the acre in certain parts of Nevada.

We may therefore reasonably consider the part which the rapid multiplication of the smaller browsing animals may have played during the Tertiary period of Europe.

Food competition especially intense on islands.—The influence of the goats on islands is cited by Wallace (1881.1, pp. 280, 283–286) and Palmer.

Palmer (1899.1, p. 89) observes:

> Sheep and goats when numerous are likely to cause widespread injury, particularly in forested regions. An instructive example of the damage done by goats is that on St. Helena, described by Wallace. St. Helena is a mountainous island scarcely 50 square miles in extent, and its highest summits reach an elevation of 2,700 feet. At the time of its discovery, about the beginning of the sixteenth century, it is said to have been covered by a dense forest; to-day it is described as a comparatively barren rocky desert. This change has been largely brought about by goats first introduced by the Portuguese in 1513, which multiplied so fast that in 75 years they existed by thousands. Browsing on the young trees and shrubs, they rapidly brought about the destruction of the vegetation which protected the steep slopes. With the disappearance of the undergrowth began the washing of the soil by tropical rains and the destruction of the forests. In 1709 the governor reported that the timber was rapidly disappearing and that the goats should be destroyed if the forests were to be preserved. This advice was not heeded, and only a century later, in 1810, another governor reported the total destruction of the forests by the goats.
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> The Santa Barbara Islands and Santa Catalina, off the coast of southern California, and the island of Guadalupe, off the Lower California coast, are utilized as ranges for goats. All these islands are dry and more or less covered with brush, but arborescent vegetation is comparatively scarce. The goats practically run wild and already exist in considerable numbers. As yet the goats have not been on the islands long enough to cause any serious effects on the vegetation, and they may never bring about the ruin which has been wrought on St. Helena. But it is scarcely possible for the islands to be grazed by goats for an indefinite length of time without suffering serious damage.

Herbivora in relation to the Carnivora.—In all the examples of recent conditions of life cited above the unrestricted feeding and rapid multiplication of small Herbivora have taken place under artificial conditions of protection of these animals from Carnivora.

It is quite possible that in certain regions under natural conditions the Carnivora may have become diminished through epidemics or other causes, thus promoting the multiplication of the smaller browsing animals, so fatal to vegetation and to the normal distribution of food supply of a country. For a long period South America was singularly deficient in Carnivora and was overrun with the smaller Herbivora.

Introduction of Carnivora.—Among the striking examples of the effects of the introduction and competition of Carnivora in past and recent times are:

1. In the Eocene epoch the true or higher Carnivora entered into competition with the lower Creodonta of Europe and North America; this was followed by the final extinction of the last of the Creodonta in the lower Oligocene.

2. In the Pliocene epoch true Carnivora, namely, the Canidae and two destructive types of Felidae—the saber-tooths (Machaerodontinae) and the true cats (Felinae)—suddenly invaded South America. They entered a faunal region which, subsequent to the extinction of the marsupial carnivores (Thylacinidae) in the Oligocene epoch, had been entirely free from large Carnivora.

3. The introduction of the dingo (*Canis dingo*) in the Australian mainland was followed by the extinction of the Tasmanian wolf (*Thylacinus*) and "devil" (*Sarcophilus*), animals which survived only in Tasmania. The fox, which was introduced into Australia, like the rabbit, has increased so rapidly that it has become a veritable menace to native life.

4. The introduction of the mongoose (*Herpestes*) in various countries has been fatal to the entire small endemic fauna.

In each instance superior mechanical adaptation, intelligence, and plasticity in respect to change of habitat have played an important part. The Carnivora, therefore, in their relation to the balance of nature, to the destruction of competing Carnivora and Herbivora, and especially in relation to the young of the larger Herbivora, form special topics for examination with regard to extinction.

Direct elimination by carnivores.—The question as to how far the mammals of prey have been a direct cause of extinction at various times of various forms of quadruped life is considerably disputed. Morris (1895.1) observes: "So far as existing evidence goes, then, it seems probable that hostile aggression, while it may have been occasionally an indirect has rarely been the direct cause of the extinction of species." A similar opinion has been orally expressed to the author by D. G. Elliot—that no wild animal causes the extinction of another wild animal directly. Such a negative conclusion may hold true of undiminished herds and of conditions where carnivorous and herbivorous animals have evolved together and, as in the evolution of the modern battleship, modes of defense have evolved simultaneously with modes of attack.

This negative view in our opinion does not hold true where newly introduced Carnivora find quadrupeds unprovided with adequate means of defense, as in the invasion of South America by carnivores from North America in late Pliocene time. Nor does it hold true of diminished herds of quadrupeds that are unable adequately to defend their young.

Therefore we must consider the Carnivora as among the direct causes of the final extinction of diminished groups or reduced herds of animals which are struggling

to maintain their numbers against adverse conditions of physical environment, such as extreme cold, heat, and drought; of changing food supply; of competition with other quadrupeds; and of epidemics. Of Carnivora as destroyers of mammalian life the best recent treatment is that of J. Stevenson-Hamilton (1912.1, pp. 160–162, 355, 357). He says:

> It seems to be one of nature's provisions that the females of most wild animals are, generally speaking, more alert and nervous than the males and therefore, in proportion to their numbers, less frequently fall victims to the stealthy cat tribe than do the solitary members of the other sex. It is thus insured that the destruction of the mothers of the race by natural means shall not exceed the due bounds of economy nor be such as to hamper or retard proper progressive increase.

Sudden introduction of smaller Carnivora.—T. S. Palmer (1899.1, pp. 93–94) has given a striking summary of the influence of the mongoose:

> The common mongoose of India (*Herpestes mungo* or *H. griseus*), * * * a well-known destroyer of rats, lizards, and snakes, was introduced into Jamaica * * * for the purpose of ridding cane fields of rats. * * * Various remedies were tried, but apparently with little success, until in February, 1872, nine individuals of the mongoose, four males and five females, from India, were introduced. These animals increased with remarkable rapidity and soon spread to all parts of the island, even to the tops of the highest mountains. A decrease in the number of rats was soon noticeable. * * * The mongoose increased, and as the rats diminished, its omnivorous habits became more and more apparent. It destroyed young pigs, kids, lambs, kittens, puppies, the native "coney" or capromys, poultry, game, birds which nested on or near the ground, eggs, snakes, ground lizards, frogs, turtles' eggs, and land crabs. It was also known to eat ripe bananas, pineapples, young corn, avocado pears, sweet potatoes, coconuts, and other fruits. Toward the close of the second decade the mongoose, originally considered very beneficial, came to be regarded as the greatest pest ever introduced into the island. Poultry and domesticated animals suffered from its depredations, and the short-tailed capromys (*Capromys brachyurus*), which was formerly numerous, became almost extinct in some of the mountainous districts. The ground dove (*Columbigallina passerina*) and the quail dove (*Geotrygon montana*) became rare, and the introduced bobwhite, or quail, was almost exterminated. The peculiar Jamaica petrel (*Aestrelata caribboea*), which nested in the mountains of the island, likewise became almost exterminated. Snakes, represented by at least 5 species, all harmless, and lizards, including about 20 species, were greatly diminished in numbers. The same thing was true of the land and fresh-water tortoises and the marine turtle (*Chelone viridis*), which formerly laid its eggs in abundance in the loose sand on the north coast. The destruction of insectivorous birds, snakes, and lizards was followed by an increase in several injurious insects, particularly ticks, which became a serious pest, and a coccid moth, the larvae of which bore into the pimento trees.

CONTRASTS BETWEEN EXTERNAL (ENVIRONMENTAL) AND INTERNAL CAUSES OF EXTINCTION

Summarizing the nature and the effect of the external (environmental) causes of extinction we may note some features in which they contrast with those peculiar to extinction from internal causes, namely:

1. In large part the external causes of extinction originate with cosmic changes—changes in the earth itself—such as the elevation or depression of the earth's surface and the extension or contraction of areas of land and water. These changes cause progressive increase of heat or cold under conditions of either moisture or dryness; progressive increase of moisture or desiccation; and consequent changes of soil, vegetation, forestation, and water supply. From these physiographic and climatic changes result the introduction of new competitors for food and new enemies, new insect pests and new diseases.

2. Under changing physiographic conditions, even though extremely gradual, many species and genera have become extinct. Secular desiccation in successive epochs of the Tertiary period, beginning in Oligocene time but intensified chiefly in late Pliocene time, gradually became fatal to most of the browsing animals—indeed, quite as destructive to them as the cold and moisture of the glacial epoch.

3. Perhaps the most distinctive feature of extinction due to external causes is that it may exterminate the fit and the unfit alike, the adaptive and the inadaptive; it may destroy rather than improve a fauna. The extinction of many forms was certainly a consequence of the extension of glacial ice in North America and in Europe and of the desiccation in Australia.

4. An equally notable feature of the external causes of the extinction of a fauna is that they have generally acted locally or in certain regions of the earth's surface only, so that a part of the fauna affected was left to survive elsewhere. For example, the extinction of the horses and the proboscideans in North and South America during Pleistocene time did not prevent their survival in the Old World.

In contrast with extinction thus arising from external causes is extinction arising primarily from internal causes, such as relative inadaptation, or unfitness, overspecialization, and irreversibility of evolution. These causes have acted simultaneously all over the world, even under uniformly favorable climatic conditions as, for example, in the extinction of the great orders of Creodonta, Amblypoda, and Condylarthra during the Eocene epoch. The extinction that originates in internal causes—that is, in relative internal fitness or unfitness—may improve a fauna by eliminating the least-adapted members instead of destroying a fauna.

INTERNAL CAUSES OF PRESERVATION AND EXTINCTION

IMMUNITY AND ADAPTATION

Conditions in Africa.—The existing conditions among the large quadrupeds of Africa are of especial interest because of the increasing evidence that the conditions in North America in Oligocene, Miocene, and Pliocene time are most closely paralleled by those that now prevail in the great upland region of Africa—the central life belt as distinguished from the coast belt.

Recent discoveries (Bruce, 1905.1) indicate that immunity from disease has been one of the most potent causes of the adaptation of animals to their environment, and that, conversely, nonimmunity has probably been one of the potent causes of their diminution and extinction. T. H. Morgan (1903.1) includes the phenomena of immunity among the adaptive processes. He states as his personal opinion, however, that certain of these phenomena could not be due to selective processes. Similarly Leo Loeb (1905.1) believes that acquired immunity can not invariably be explained as an adaptive phenomenon.

Variations in immunity.—In Africa certain diseases are fatal to both wild and domesticated animals; others are fatal to domesticated animals but not to wild animals. Some animals succumb to certain diseases through successive generations; others, especially "natives," acquire immunity in the second generation. Still more remarkable is the fact that both wild and domesticated immunes may act as reservoirs of disease organisms which, through flies or ticks, may be carried to nonimmunes. The wild ruminants of Africa among the Bovidae especially—the buffalo (*Bos* (*Bubalus*) *caffer*), the kudu (*Strepsiceros kudu*), the wildebeest (*Connochaetes*)—carry about in the fluid portion of their blood, without themselves suffering any harm, certain protozoan trypanosomes which are fatal when borne by flies to domesticated horses (Equidae), dogs (Canidae), and cattle (Bovidae).

Thus causes favorable either to the genesis of disease organisms or to the acquirement of immunity or to the propagation and distribution of flies and ticks become matters of prime interest in relation to extinction.

Origin of immunity as a "unit" character.—For the student of extinction an important point to note in connection with "horse sickness" is that although means of artificial immunity are thus far undiscovered degrees of immunity and of natural immunity sometimes occur. Such variations in respect to immunity would in a state of nature lead to the survival or gradual selection of immune forms and the consequent production of immune races.

BULK NOT INHERENTLY INADAPTIVE

Bulk supposed to be inadaptive.—There is a widespread belief or tradition that bulky animals have tended to disappear first—that bulk is in itself inadaptive. Thus Owen, although as late as 1877 (1877.1, pp. ix–x) disposed to attribute the extinction of the large mammals of Australia to the agency of man, advanced the theory that bulky size may be a disadvantage under changed conditions. He writes:

> In proportion to the bulk of a species is the difficulty of the contest which, as a living organized whole, the individual of such species has to maintain against the surrounding agencies that are ever tending to dissolve the vital bond and subjugate the living matter to the ordinary chemical and physical forces. Any changes, therefore, in such external conditions as a species may have been originally adapted to exist in will militate against that existence in a degree proportionate, perhaps in a geometrical ratio, to the bulk of the species. If a dry season be gradually prolonged, the large mammal will suffer from the drought sooner than the small one; if any alteration of climate affect the quantity of vegetable food, the bulky herbivore will first feel the effects of stinted nourishment. * * * The actual presence, therefore, of small species of animals in countries where larger species of the same natural families formerly existed is not the consequence of any gradual diminution of the size of such species but is the result of circumstances which may be illustrated by the fable of the "oak and the reed"; the smaller and feebler animals have bent, as it were, and accommodated themselves to changes which have destroyed the larger species.

Morris observes (1895.1, p. 254):

> One tendency, which has particularly manifested itself in herbivorous animals, has frequently led directly to their destruction. This is the tendency to increase in size through the double influence of abundance of food and little waste of tissue through exertion. In the sluggish grass eaters, dwelling on plains covered with rich herbage, or leaf and twig eaters in tropical forests, the nutritive agencies are in excess of those of waste, and these animals seem always to have tended to an increase in size, until those of least exertion and greatest powers of obtaining food became enormous in dimensions. An example of the same kind among the Carnivora is the Greenland whale, which, while feeding on minute forms, obtains them in enormous quantities with little muscular exertion and has in consequence become of extraordinary dimensions.

Statistics as to handicap of bulk.—This general opinion as to the fatality of bulk in mammals is open to question. When we examine the matter statistically we find that a far larger number of families of small mammals have become extinct than of large mammals. The only families of bulky land mammals that have become entirely extinct since the beginning of Tertiary time are the following:

Families of bulky land mammals that have become extinct since Cretaceous time

Family	Extinct in—	Region
Coryphodonts	Lower Eocene	Holarctica.
Uintatheres	Upper Eocene	North America, Asia.
Titanotheres	Lower Oligocene	Holarctica.
Pyrotheres	Eocene	South America.
Lophiodonts	Upper Eocene	Eurasia.
Barytheres	Upper Eocene	North Africa.
Arsinoitheres	Lower Oligocene	North Africa.
Elotheres	Lower Miocene	North America.
Amynodonts	Lower Oligocene	North America.
Chalicotheres	Lower Pliocene	Eurasia.
Diprotodonts	Lower Pleistocene	Australia.
Giant sloths (3 families).	Pleistocene	North and South America.
Glyptodonts	Pleistocene	North and South America.
Toxodonts	Pleistocene	South America.

Number of extinct and surviving families of large and of small mammals since Cretaceous time

	Families extinct	Families surviving	Percentage surviving
Large	16	9	36
Intermediate and small	48	90	65

The above figures would seem to indicate that the chance of survival of small mammals is nearly twice that of the survival of bulky mammals, but when we consider that many extinct families of small mammals remain to be discovered among the Marsupialia, Insectivora, Cheiroptera, and especially the Rodentia, the disparity indicated by the figures given is not so great.

Among the large surviving land mammals are the families of elephants, hippopotami, rhinoceroses, giraffes, elands, and elks, and among the sea mammals are walruses and the various families of Cetacea, which, so far as known, are the largest mammals of all time.

Further, we may recall the facts (1) that in lower Eocene time the small Condylarthra became extinct far earlier than the large Amblypoda; (2) that in lower Oligocene time many families of small Artiodactyla and Perissodactyla became extinct at the same period as the large titanotheres, lophiodonts, and amynodonts; (3) that in Pleistocene time the relatively small *Mylodon* disappeared as early as the large *Megatherium;* (4) that the extinction of the mammoth in North America during or after the glacial epoch attracts attention because of the animal's large size, but, as indicated above, many smaller quadrupeds disappeared at the same time—for example, the horses and the sloths.

Bulk and slow breeding not inimical to rapid evolution.—The following arguments of Wallace and of Andrews in regard to bulk and slow breeding are in part fallacious and receive little support from paleontology. Wallace remarks (1876.1, vol. 1, pp. 158–159):

> There is, however, another cause for the extinction of large rather than small animals whenever an important change of conditions occurs, which has been suggested to me by a correspondent but which has not, I believe, been adduced by Mr. Darwin or by any other writer on the subject. It is dependent on the fact that large animals as compared with small ones are almost invariably slow breeders, and as they also necessarily exist in much smaller numbers in a given area, they offer far less materials for favorable variations than do smaller animals In such an extreme case as that of the rabbit and elephant, the young born each year in the world are probably as some millions to one; and it is very easily conceivable that in a thousand years the former might, under pressure of rapidly changing conditions, become modified into a distinct species, while the latter, not offering enough favorable variations to effect a suitable adaptation, would become extinct.

The above argument, however, is not in accord with the facts; the slow-breeding elephant evolved with far greater rapidity than the swift-breeding mouse.

C. W. Andrews has recently (1903.1, p. 2) revived this argument that the lengthening of the time taken to attain sexual maturity may affect the rate of evolution and under changed conditions where a rapid rate of evolution is essential may cause extinction. He writes:

> In many ungulates this increased longevity is indicated by various modifications of the teeth, tending to give them a longer period of wear: generally this end is attained by the increasing hypselodonty of the cheek-teeth. A necessary consequence of the longer individual life will be that in a given period fewer generations will succeed one another, and the rate of evolution of the stock will therefore be lowered in the same proportion. If now the conditions of life undergo change, the question whether a given group of animals will survive or become extinct will depend upon whether it can undergo sufficiently rapid variation to enable it to avoid getting so far out of harmony with its surroundings that further existence becomes impossible. It seems to follow, then, that the smaller animals, in which the generations succeed one another rapidly, will have a better chance of surviving than the larger and more slowly breeding forms, which at the same time will be still further handicapped if, as is usually the case, they are more highly specialized than the smaller forms and therefore have a more restricted range of possible variation.

This argument is contradicted by all the facts of paleontology: there is no relation between rapid breeding and rapid evolution.

As against these purely hypothetical considerations paleontology shows that during Pliocene and Pleistocene times the slow-breeding Proboscidea evolved quite as rapidly if not more rapidly than the rapid-breeding Rodentia.

Relation of bulk to nutrition.—Stromer (1905.1, pp. 97–132) discusses in detail the relation of bulk to nutrition. He observes that nourishment or lack of it must not be overestimated as a factor in extinction, for it has been shown among mammals that the nourishing surfaces are only squared as the mammals increase in size, while the bulk of the body is cubed, and that small forms eat much more relatively than large forms. The fact remains that the great terrestrial animals need as a rule a large amount of vegetable food and also an abundance of water. Aquatic mammals, on the other hand, embrace more giant carnivores (cetaceans, walruses) than herbivores (hippopotami, *Rhytina*). Naturally, defenseless giant forms incapable of fighting can maintain their existence only in the absence of destructive Carnivora—for example, the giant rodent (*Amblyrhiza*) of the Lesser Antilles. Such factors as the diminution of food supply would weigh much more heavily against ponderous animals like *Glyptodon* and *Megatherium* than against agile ones such as giraffes, elephants, and rhinoceroses. While the glacial epoch may have destroyed the northern representatives of *Hippopotamus*, it must be recalled that this genus at

the same time became extinct in India, Java, and Madagascar, while many of the large European mammals survived the glacial epoch. Some very large animals, such as the elephant, for instance, have been shown to be very adaptable. At the present time the elephant is found in the damp jungle and parklike districts, in tree and bush steppes, in low-lying plains, on plateaus and mountains. Salensky (1905.1) has lately shown that the mammoth was fully adapted to life on grassy plains of high latitudes. The mastodon also occupied many different life habitats.

Conclusions as to effect of bulk.—Our conclusion is that bulk is not intrinsically or per se fatal. All the bulky mammals which have disappeared have possessed some single inadaptive organ or set of organs which it seems probable would have proved equally fatal to animals of small size; they have lacked in intelligence, resourcefulness, or brain power; they have specialized to an extreme in certain directions; they have reached a point where there was only a single mode of living left to them, and when this was altered or when a particular source of food supply was cut off they perished with it. On the other hand, intelligent, resourceful, and adaptively constructed large mammals, like the elephant, have survived great physiographic and biotic changes. Presence or absence of such adaptations is almost equally fatal to small animals; bulk in itself is not a cause of extinction; inadaptive bulky animals have disappeared side by side with the inadaptive diminutive animals.

The chief inadaptations of large mammals are the following: (1) Disadvantage of the large amount of food required by a large animal, which is offset by the advantage that many large animals can travel long distances; (2) diminished birth rate, which is a characteristic of large animals, is a point to be noticed; as a rule, the larger the animals the fewer the young and the less able a species would be quickly to regain numerical strength after some widespread diminution in number; the diminished birth rate is, however, offset by greater longevity and greater power to protect young from enemies. Darwin (1859.1, p. 64) observes:

> The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase; it will be under the mark to assume that it breeds when 30 years old and goes on breeding till 90 years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive 15 million elephants, descended from the first pair.

VALUE OF SINGLE ORGANS IN SURVIVAL OR EXTINCTION

Percentages of natural increase and decrease.—Recent conditions among the large African mammals as observed by Stevenson-Hamilton (1912.1, pp. 9–95) show the effects of numerical reduction and the highly varied action of the same causes on different stocks and different organs. As to numerical increase or decrease the author estimates (p. 10) that (1) the actual net annual increase of stock of the larger antelopes under ordinary favorable natural conditions is not above 5 per cent; (2) in a region where the carnivorous animals have been destroyed or reduced in number the net annual increase is about 10 per cent; (3) the gross natural increase of the larger antelopes in ordinary years is 20 per cent, which is offset by the death annually of 5 per cent from old age and the destruction of 15 per cent by the Carnivora, especially the young and worn-out animals; (4) anything that checks the gross natural increase and hastens the natural decrease means the permanent reduction and perhaps the final extinction of the stock. This balance affects the survival or elimination value of single organs.

Extinction of Artiodactyla.—Woldemar Kovalevsky, a Russian paleontologist, was one of the pioneers in the consideration of the survival or extinction value of single organs. He observes, in his great monograph (1876.1, p. 152), that the extinction of all Artiodactyla having an inadaptive foot structure and inadaptive grinding teeth occurred as follows: Upper Eocene: *Xiphodon*, *Anoplotherium*, *Diplopus*; Oligocene: *Hyopotamus*, *Anthracotherium*, *Entelodon*. He pointed out that the inadaptation of the foot in these animals consisted of a mechanical defect in the manus, the third metacarpal not spreading above to articulate with the trapezium as in the adaptive manus of the pig and hippopotamus, and that the inadaptation in the grinders consisted of the persistent short or brachyodont crowns, bunoselenodont and bunodont, composed of partially rounded cones. The feet, being mechanically weak in the function of the carpals and metacarpals, were incapable of the elongation into cannon bones, a cursorial or speed adaptation which saved the lives of artiodactyls with the adaptively reduced digits. The short teeth were by his theory not adapted to a supposed change of vegetation from softer herbage to harder Gramineae. His paleozoologic supposition that such a change of food occurred was independently confirmed by the paleobotanists Saporta and Marion. His conclusion as to single organs causing extinction (which was original) has since been abundantly confirmed by subsequent observations of the extinction of all forms of quadrupeds having these inadaptive types of short-crowned grinders, both in North America and in India.

Inadaptation of cone and crescent teeth.—The bunoselenodont or cone and crescent molar pattern is typified in the titanotheres and consists of one or two detached cones on the inner side of the upper grinding teeth and of two crescents on the outer side. It is adapted to browsing on coarse, soft food rather than on hard, fine food.

This dental type presents a cul de sac of evolution, because it is incapable of transformation either into

the elongate or hypsodont grazing type or into the lophodont or crested type. In the absence of transverse crests between the inner cones and the outer crescents elongation would produce a number of separate columns and crescents.

It is interesting to observe, in the evolution of the titanotheres, the attempt of nature to create a hypsodont crown out of this cone and crescent type by the elongation of the crescents on the outer side of the superior grinding teeth. The inner cones do not share in this elongation; the result is a tooth half hypsodont and half brachyodont, obviously a very poor mechanism.

The bunoselenodont tooth was therefore incapable of further evolution in any direction; no mechanical progress or perfection was possible.

Against the theory that the form of the teeth alone caused the extinction of these great animals we must record the fact that the giant elotheres of lower Oligocene time, which had teeth that were still less effective (of an all-cone pattern), survived to a later geologic period than the titanotheres. If we knew all about the life of these elotheres we should probably find that they had some compensating advantage in local habitat, perhaps recourse to river-border life.

The hypothesis that the bunoselenodont tooth pattern was, if not the sole, at least a potent cause of extermination is supported by strong collateral evidence, which is presented in the accompanying diagram (Pl. XLVIII). It appears that all bunoselenodont quadrupeds, whether belonging to the Artiodactyla or the Perissodactyla, disappeared during the Oligocene epoch or early in the Pliocene. The only bunoselenodont mammals that survived are the chalicotheres, which persisted in the Northern Hemisphere until the end of Pliocene time, probably in a forest habitat. The defective tooth structure in these animals was probably compensated for by the development of giant claws on the feet, which gave these strange quadrupeds certain advantages similar to those that were enjoyed by the giant sloths.

Elongation (hypsodonty) of the molar teeth in relation to longevity and reproductive power.—The elongation of the molar teeth is obviously a direct advantage in the promotion of longevity and fertility, an advantage that might lead to selection of fluctuations in length. The elongate crowns of the teeth of the elephants and the horses enable individuals to live many years and to produce a large number of young. Elephants, which are provided with successive long-crowned teeth, live, according to Darwin, between 90 and 100 years and, although slow-breeding animals, produce a large number of young. Horses, which have long-crowned teeth, live to the age of 25 years and, foaling every year, multiply with great rapidity.

In contrast, an animal like the titanothere *Palaeosyops*, with its short-crowned teeth, would live a comparatively short time and produce comparatively few young. Through long periods of geologic time this relation of longevity to reproduction would tend in the same habitat to replace races that had short-crowned teeth and that were therefore short lived with races that had long-crowned teeth and that were therefore long lived.

As a matter of fact, this theoretical condition is modified by change of habitat, because we observe that the short-crowned Cervidae of browsing habits hold their own in the forests and that the generally long-crowned Antilopidae are perfectly adapted to life on the plains.

Inadaptation of small brain.—The chief advantages of brain capacity undoubtedly appear in relation to adaptability of habit and resourcefulness in times of exposure, to alertness in avoiding new dangers to which the young may be exposed, and to enterprise in seeking new habitats, qualities that are especially valuable at times of climatic change and of severe competition.

Modern quadrupeds differ widely in regard to resourcefulness under adverse conditions of environment, as illustrated on the western plains during the great winter storms. When sheep, cattle, and horses meet the unexpected conditions incident to a blizzard, the sheep disappear first, the cattle second, the horses last—that is, the horses, largely owing to instincts which they have inherited from northern ancestral strains, meet new conditions of life in most extraordinary ways, whereas cattle of southern wild ancestral strains are far less resourceful.

The paleontologist knows nothing of the psychic qualities of an extinct animal; he can judge its brain power only by examining its intracranial cast, which often reproduces the size and external form of the brain with exact fidelity. Lartet, following Cuvier, was among the first to allude to the law of progressive cerebral development of certain of the Tertiary mammals. He says (1868.1, pp. 1120–1122):

> Il résulterait en effet d'un certain nombre d'observations relevées à divers étages de la stratigraphie tertiaire, que, plus les mammifères remontent dans l'ancienneté des temps géologiques, plus le volume de leur cerveau se réduit par rapport au volume de leur tête et aux dimensions totales de leur corps. * * * On a dit que les plus grands mammifères sont ceux qui vivent le plus longtemps; ce qui serait plus près de la vérité, c'est que la longévité normale paraît s'accroître en raison directe du volume absolu du cerveau.

Marsh in 1884 considered brain size in relation to the final extinction of the uintatheres. He observes (1884.1, p. 190):

> The small brain, highly specialized characters, and huge bulk rendered them incapable of adapting themselves to new conditions, and a change of surroundings brought extinction. * * * The Dinocerata, with their very diminutive brain, fixed characters, and massive frames, flourished as long as the conditions were especially favorable, but with the first geological change they perished and left no descendants

In discussing the brain, especially after referring to the general law of brain growth (that is, evolution) during the Tertiary period, he states:

> To this general law of brain growth two additions may now be made, which, briefly stated, are as follows: (1) The brain of a mammal belonging to a vigorous race, fitted for a long survival, is larger than the average brain, of that period, in the same group; (2) the brain of a mammal of a declining race is smaller than the average of its contemporaries of the same group.

The ratio of brain weight to body weight in recent mammals has been made the subject of an exhaustive investigation by Max Weber (1896.1), who publishes the ratios between brain weight and body weight in thirteen existing orders of mammals. In general, (1) small mammals have relatively larger brains than large mammals; (2) within a natural order brain weight does not increase relatively with body weight; (3) in growing individuals the relative brain weight decreases; (4) in absolute brain weight man is exceeded only by the Proboscidea and Cetacea, in relative brain weight man is exceeded only by certain of the small mammals; (5) in the very primitive marsupials the ratios of brain weight to body weight vary from 1:110 to 1:711 as compared with the Carnivora, in which the ratio varies from 1:100 to 1:546. Brain weight, however, does not register the great disparity in intelligence as a survival factor between the Marsupialia and the Carnivora fissipedia.

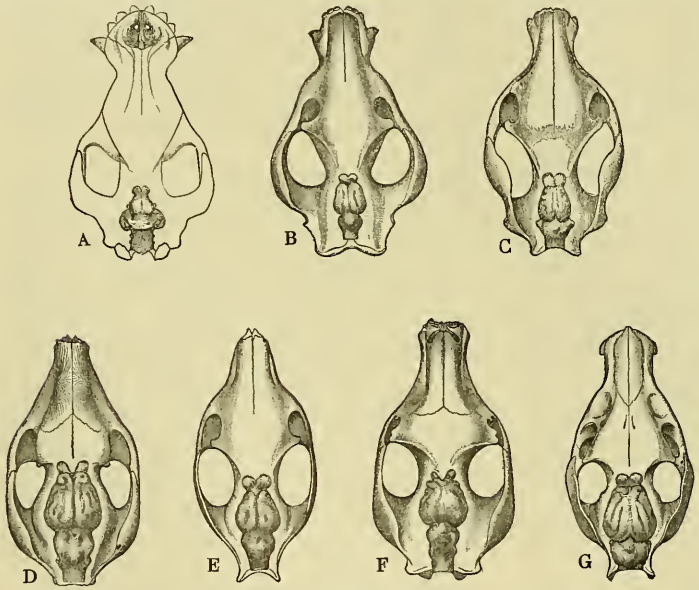

FIGURE 760.—Brain proportions in Eocene perissodactyls, an artiodactyl, and an amblypod of similar size

A, *Coryphodon hamatus;* B, *Limnohyops laticeps;* C, *Palaeosyops robustus:* D, *Colonoceras agrestis;* E, *Hyrachyus bairdianus;* F, *Amynodon advenus;* G, *Eporeodon socialis.*

The chief measure of the brain capacity of extinct mammals is indicated by (1) absolute size and weight of the brain, (2) ratio of brain weight to body weight, (3) development of the cerebral convolutions, (4) proportion between the frontal and parieto-occipital lobes of the cerebrum.

Exceptions: certain small-brained types survive.—The series of diagrams in Plate XLIX shows the enormous contrast between the brains of a number of Eocene mammals and those of a number of existing mammals of equal size and equal bulk. The contrast is drawn between pairs of animals of somewhat similar habits of life. Thus the Eocene *Arctocyon* (A) is contrasted with the existing dog (*Canis*), the Eocene *Phenacodus* (B) is contrasted with the domestic pig (*Sus*), both animals possessing bunodont teeth and somewhat similar omnivorous feeding habits. The Eocene *Coryphodon* (C) is contrasted with the existing rhinoceros. Finally the Eocene *Uintatherium* (D) is contrasted with the Oligocene titanothere *Menodus giganteus.*

The brains of the archaic mammals shown on the left in Plate XLIX (*Arctocyon, Phenacodus, Coryphodon, Uintatherium*) are not only extremely small in proportion to the size of the animals but are of a low type; they have large olfactory lobes, small cerebral hemispheres, with small frontal lobes; and they are relatively smooth—that is, they are without convolutions.

An equally intrinsic inadaptation seems to have been the incapacity for progressive increase in size of brain in successive geologic periods; in other words, the brain and consequently the psychic powers appear to be in a condition of arrested development. The only exception to this rule is seen in one family of archaic creodonts, the Hyaenodontidae, in which the brain attained considerable size in the surviving members of lower Oligocene time.

This limited brain power and arrested brain evolution placed these archaic quadrupeds at a great disadvantage in competition with the more advanced placental mammals, which suddenly appeared in lower Eocene time. The cursorial Phenacodontidae measured their psychic powers with the cursorial Equidae; the small-brained Creodonta generally competed with the incoming true Carnivora, with their progressive increase in size of brain.

The long survival and steady increase in size of the clumsy Amblypoda—*Pantolambda* (basal Eocene),

Coryphodon (lower Eocene), and *Uintatherium* (upper Eocene)—despite arrested brain development, is one of the most astonishing phenomena of Eocene mammalian life. Their survival may be accounted for by the development of very effective defensive weapons, the tusks and horns wherewith they stood off their enemies and protected their young. The final extinction of these mammals may be attributed to two causes—low brain power, which may have inhibited the proper defense and care of the young, and the arrested evolution of the grinding teeth, which were actually no larger and little more effective for the comminution of food in the giant Dinocerata of upper Eocene time than in the smaller *Coryphodon* of lower Eocene time.

In a race that especially develops tusks and horns, both probably favored by sexual selection, the grinding teeth tend to show arrested evolution. The disappearance of the small phenacodonts long prior to that of the large Amblypoda is another illustration of the fallacy of the widespread belief that bulky animals tend to disappear first.

The competition of the archaic small-brained creodont Carnivora with the diminutive large-brained pro-Carnivora in Eocene time may be only remotely compared with the extinction of the Tasmanian wolf (*Thylacinus*) and Tasmanian "devil" (*Sarcophilus*) through the introduction of the true dog (*Canis dingo*) on the Australian mainland. The steady increase in size of the creodont carnivores, as displayed in *Patriofelis* and the enormously powerful *Harpagolestes*, may be placed parallel with the increasing size of the equally small-brained Amblypoda.

Exceptions: large-brained types perish.—Against this strongly cumulative evidence that the brain is one of the single organs whose development has been a decisive factor in the preservation or extinction of races of animals we must place certain exceptions. The extinct short-limbed rhinoceros (*Teleoceras*) of the upper Miocene evidently had a larger brain than the surviving true rhinoceros. Again, it appears from intracranial casts that the Pleistocene mastodon of North America had a brain fully as large as that of the existing elephants. In both *Teleoceras* and the mastodon great cerebral development failed to preserve the race. Conversely, certain very small-brained animals, notably the North American opossums (Didelphiidae) and the Insectivora, have survived, even to the present time. The interpretation put upon these exceptions is that a large cerebral development may be insufficient to compensate for the possession of certain disadvantageous organs.

INADAPTATION OF EXTREME SPECIALIZATION

Extreme specialization may constitute a chain of causes that lead to extinction. An animal may specialize to an extraordinary degree in a single mode of subsistence, and the food upon which it subsists may be diminished or destroyed; or a race of animals may expend its energy largely in the development of certain single organs, such as horns or tusks, which become dominant and interfere with the proper development of other organs. If a race undergoes a marked degeneration or loss of organs it can not retrace its steps, because, to use Dollo's dictum, evolution is irreversible—that is, lost parts can not be regained.

SURVIVAL OF THE UNSPECIALIZED

The extinction of the highly specialized has been so frequently observed that it was formulated into a law by Cope (1896.1, p. 173):

> Agassiz and Dana pointed out this fact in taxonomy, and I expressed it as an evolutionary law under the name of the "doctrine of the unspecialized." This describes the fact that the highly developed or specialized types of one geologic period have not been the parents of the types of succeeding periods, but that the descent has been derived from the less specialized of preceding ages. No better example of this law can be found than man himself, who preserves in his general structure the type that was prevalent during the Eocene period, adding thereto his superior brain structure.
>
> The validity of this law is due to the fact that the specialized types of all periods have been generally incapable of adaptation to the changed conditions which characterized the advent of new periods. Changes of climate and food consequent on disturbances of the earth's crust have rendered existence impossible to many plants and animals and have rendered life precarious to others. Such changes have been often especially severe in their effects on species of large size, which required food in large quantities. The results have been degeneracy or extinction. On the other hand, plants and animals of unspecialized habits have survived.

IRREVERSIBLE EVOLUTION

As shown above in the discussion on bunoselenodont teeth, an organ must be capable of development in a new direction to supply the new needs of the organism; if the organ is lost, degenerate, reduced, or mechanically incapable of further development it constitutes a bar to the survival of its possessor (Dollo, 1893.1). For example, a change of vegetation in Oligocene time appeared to favor the animals that were capable of cropping their food as well as grinding it up into fine particles with the molar teeth. This change found the titanotheres possessed of rounded, button-like incisor teeth, totally useless for cropping. This loss of useful cropping teeth may not have been compensated for, as it was with the square-lipped grazing rhinoceroses, by the evolution of effective upper and lower lips. It may be said, therefore, that the titanotheres had lost all power of adaptation to grazing habits through the degeneration, simplification, or absence of their incisor teeth.

INADAPTATION OF DOMINANT ORGANS

Organs that have reached a stage of development so extreme as to require a larger share of the sum total of bodily nutrition than their general or apparent

utility justifies may be known as dominant organs. They violate the St. Hilaire law of economy of growth and compensation of parts, or the highest combination of adaptable structure through the subservience of each organ to all the other organs. The great horns of the titanotheres, the giant horns of the Irish deer (*Cervus megaceros*), the single tooth of the narwhal (*Monodon*), the giant tusks of the elephants are examples of dominant organs.

The very development of such organs has long been considered one of the possible causes of extinction, We immediately observe that certain dominant organs. like the tusks of the elephant, serve a great variety of useful purposes; they are by no means developed solely for service in the struggle between the bulls for possession of the females. Again, if large horns are considered fatal, it is noteworthy that the small-horned titanotheres (*Menodus*, *Brontops*) disappeared simultaneously with the long-horned titanotheres (*Brontotherium* and *Megacerops*). Were it not for this fact we might have attributed the extinction of the titanotheres to the possession of such apparently useless dominant organs as their horns.

SELECTION OF SEXUALLY DOMINANT ORGANS

The general explanation that has been offered for certain dominant characters peculiar to the males is that they have been developed or perhaps over-developed, through the competition of the males for the possession of the females. Thus, in respect to horns, incisor and canine tusks there has been an incidence of selection on organs that were employed for combat between males and that were of little or no use at other times except in standing off carnivorous enemies.

Noteworthy facts derived from our study of the titanotheres are that the horns first arise alike in both sexes as rudiments, or extremely small horns; that they appear to be equally developed in the males and the females; and that they gradually become distinctively male characters, so that the sexes are sharply separated by the size and development of the horns. The horns were undoubtedly of advantage to the males in their sexual combats for the possession of the females, and a constant selection of individuals with the largest horns may have been in process. This main emphasis of natural selection on characters which are useful for competitive and combative purposes, it is argued, may have been the cause of the arrested evolution of the grinding teeth.

It is certainly true that the grinding teeth attained a higher mechanical perfection in the short-horned titanotheres than in the long-horned brontotheres, and this would serve to prove that in the menodonts the teeth were being favored by selection, while in the brontotheres the horns were being favored by selection. As noted above, the superiority of the menodonts in the matter of tooth structure did not save them from the extinction which overtook the brontotheres.

CAUSES OF OVERDEVELOPMENT

Naturalists generally have attributed overdevelopment to the selection of favorable fluctuations in size, but Cope (1896.1, p. 480) invoked a certain kind of intrinsic hereditary force. He says: "I have therefore assumed as a working hypothesis the existence of the bathmic energy and have inquired how far the facts in our possession sustain it." Similarly, the over-development of dominant organs has recently been explained by F. B. Loomis (1905.1, p. 843) as the result of "momentum." After discussing many known instances of organs that appear to have passed a stage of utility, he observes:

> The above are selected examples in which a feature once useful has been developed beyond its maximum utility. Many others equally striking might be cited, the explanation of all of which is extremely difficult unless such a factor as momentum is called in. In the light of this factor, however, a logical and apparent cause is found. Momentum also explains why a character that originated in accordance with the environment develops so rapidly, and why, when an animal had reached adjustment to its surroundings, it still goes on beyond a perfect adjustment. It may be laid down as a rule, then, that a variation started along any line tends to carry that line of development to its ultimate, being driven by momentum. If the feature is detrimental the group dies out; if, however, it is merely a minor feature it makes a handicap. A line of development may be stopped and its momentum overcome, but the tendency is to keep right on.

RATES OF BREEDING AND EXTINCTION

It has already been shown that failure or inability to protect the young, or possibly the inhibition of fertility through low temperature, must be among the causes of extinction, and as extinction rapidly follows when the death rate exceeds the birth rate, the rate of breeding must be considered in any inquiry as to extinction. Arthur Erwin Brown, in a letter written October 24, 1907, has called the attention of the writer to this subject and has contributed some valuable notes. He observes:

> The thought suggests itself that the long breeding period may have been a factor in the decline of the Perissodactyla. In all perissodactyls gestation is slow. Hodgson 70 years ago gave the Indian rhinoceros 17 to 18 months; it does not appear that these figures have been amended.

Dr. Frank Baker, late superintendent of the National Zoological Park at Washington, fixed the gestation of *Tapirus terrestris* at 396 days. The gestation period of such an animal as the tapir, adapted to the long summers and short winters of temperate climates, would naturally be unadapted to the long winters and short summers of the glacial climates of Pleistocene time; consequently the extinction of the Tapiridae in North America during late Pleistocene time may have been due to the exposure of the newly born young to climatic conditions to which they were not adapted.

Stevenson-Hamilton (1912.1, p. 44) observes that the gestation period of the African antelopes is about eight months. Most females seek sheltered spots before calving. About calving time great destruction is wrought by the Carnivora, especially by the hunting dogs (*Lycaon pictus*), which run down the little antelopes with great ease and destroy large numbers of them. Within a very few days of birth all young antelopes and zebras are capable of keeping up in the most surprising manner with the fully grown animals even when the latter are going at full speed. (See p. 846.)

SELF-EXTINCTION THROUGH ARRESTED VARIATION

The Italian geologist Brocchi (1814.1, vol. 1), the author of an able work on the fossil shells of the sub-Apennine hills, advanced the hypothesis of some regular, constant law by which species may disappear from the earth gradually and in succession. The death of a species, like the death of an individual, he suggested, may depend upon certain peculiarities of constitution conferred upon the species at its origin, and as the longevity of the individual depends upon a certain force of vitality, which after a period grows weaker and weaker, so the longevity of the species may depend upon the quantity of prolific power originally bestowed upon it; after a season the species may decline in energy and its fecundity may be gradually lessened from century to century.

Lyell opposed this doctrine on the ground that there is seldom evidence of physiological deterioration in the last representatives of a species.

Neumayr also opposed this doctrine. He remarks (1889.1, vol. 1, pp. 142–143, 147):

> It has been assumed that species, like individuals, go through a prescribed cycle of life, that they arise, flourish, decline, and die, unless they undergo a sort of rejuvenation through gradual variation, and thus extinction has been attributed to the inability to continue to vary. It is undeniable that countless forms have become extinct because they could not adapt themselves rapidly enough to changing conditions, even where these changes covered thousands of years. However, paleontology affords no proof—nor is any evidence to be found elsewhere—for the more extreme view that forms maintain their power to vary for only a limited time, after which they become rigid and unadaptable. That any animal ever ceased to show variations is a purely arbitrary assumption [p. 143]. Nor is the analogy between decay and death of the individual and of the species or family justified, for senile degeneration and death are by no means peculiar to all living organisms. Among the Protozoa death is the result of external violence, not the necessary outcome and prescribed end of the life cycle, and only among the higher organisms with more complicated methods of reproduction does it become so. In every instance extinction can be explained on the basis of the struggle for existence and without recourse to any mysterious inner causes [p. 147].

The idea that self-extinction is caused by an inherent arrest of variation was expressed in another form by Darwin and Wallace, namely, that, as a limitation or cessation of variation would cut off material for improvement through selection, a fixed or nonadaptable type would arise, and extinction would follow. It has been revived or discussed by Döderlein (1888.1), Rosa (1903.1), Abel (1904.1), Plate (1904.1), and Stromer (1905.1). The rôle assigned to the limitation of variation (independent of the effects of environment) as a cause of extinction again depends upon direct observation as to the modes of evolution. If there is a hereditary progressive trend (such as "Mutationsrichtung") in evolution leading in certain directions, is there also an arrest of such movement?

Döderlein (1888.1, p. 394) advanced the opinion, especially as a consequence of certain opinions of Cope, that in a long-continued evolution in one direction there is inherited not so much a definite condition as a tendency to continue to develop in that direction. In spite of the law of inertia (Trägheitsgesetz) this inherited tendency continues even if it is no longer useful to the organism unless it is offset by powerful counterforces, such as natural selection under conditions of severe competition. Thus organs may arise that are directly harmful to their possessors and may contribute to their destruction, as, for instance, the excessively large canines of the last machaerodont tigers and the gigantic antlers of *Cervus eurycerus* and *C. dicranius*.

Rosa (1903.1) discussed the hypothesis of the progressive reduction of variability and emphasized the fact that highly specialized organisms may show variations but that these variations do not lead to new phyla, or, if they do, only to a slight extent.

Plate's discussion and criticism (1904.1, pp. 641–655) of Rosa's views is as follows:

> Daniel Rosa in 1899 published a paper [1899.1] attempting to prove that there is a progressive reduction of variability in species, which leads ultimately to their extinction. In the first place, Rosa bases his "law" on the fact that evolution in many cases means a constantly increasing specialization. Species tend to adapt themselves more and more closely to definite environmental conditions and become ever more specialized. The smaller the circle of external factors to which a species is adapted, the more limited becomes its "phylogenetic capacity" (Rosa), the capacity to produce new and distinctly different species. As pointed out by Cope in his "law of the unspecialized," the great phylogenetic lines originated in unspecialized forms with great potential adaptability. But the struggle for existence drives organisms into more and more extreme specialization, thereby diminishing their chances of becoming stem forms of great phylogenetic lines. Therefore one may speak of a "law of progressive specialization." Rosa calls it the "law of progressively diminished variation" and extends its application beyond the cases of very highly specialized forms. * * *
>
> However, instances like that of the African elephant, which shows several geographic varieties, go to prove that highly specialized genera do not lose the power to produce new species, although they can obviously not become the originators of entirely new and divergent groups. Thus specialization limits the "breadth of evolution" (Evolutionsbreite) but does not, as maintained by Rosa, check evolution itself. * * *
>
> Rosa goes on to set up a law of progressively diminished variability as the cause of progressively diminished variation.

This leads directly to the further assumption that every species approaches its constant form (Rosa, p. 58). Thus he supposes that through inner causes, which we are at present unable to analyze, the power to vary gradually vanishes in the course of evolution, and that every phyletic series leads finally to rigid forms, which, being unequal to any further changes in their environment, are doomed to extinction. * * *

Rosa's law of progressively diminished variability is based on a fallacy, for, except in cases of parasitism, etc., evolution leads to greater and greater complication, and variability, which in general depends on the number of variable elements, increases as the number of tissues and organs and the number of their characters is augmented. If, as Rosa maintains, variability and the number of variable elements became progressively reduced in the course of evolution, the higher organisms could not have been derived from the lower.

In high specialization, as for instance, when the primitive mammalian foot is converted into the fossorial extremity of the mole, the saltatorial extremity of the kangaroo, or the cursorial extremity of the horse, many characters are no doubt lost and variability appears to be diminished, but this is only the negative aspect, and in reality these adaptations are due to the acquisition of new characters by certain structures. * * *

Rosa conceives of the splitting up of forms into families, genera, and species as a distribution among the descendants of possible variations a, b, c, d, e, . . . z, of every organ of the stem form. Thus one phyletic series will have the possibilities a–f, another g–o, a third p–z with respect to the same organ—for instance, the foot. The end result in each case will be rigid forms, one with the foot a, another with h, a third with k, etc. This conception is erroneous. As a matter of fact, the stem form is split up into new species by the acquisition of new characters, but not by a distribution of variations among the various groups of descendants.

Thus, finally, while Rosa is right in holding that highly specialized species readily become extinct under altered environmental conditions, he is mistaken in believing that variability itself is limited by a one-sided organization. Variability has nowhere been wholly wanting; it has merely worked too slowly and too incompletely at times to prevent extinction. Therefore not only megatheres and ichthyosaurs but countless simple Protozoa, coelenterates, and echinoderms as well have become extinct.

Similarly, C. B. Crampton (1902.1), as cited by C. W. Andrews (1903.1, p. 1), suggests internal causes of extinction as follows:

> In a recent paper by Mr. C. B. Crampton a possible inherent cause of extinction is suggested. It is impossible to do justice to this interesting paper in a short note, but the gist of the argument seems to be as follows: In the original unicellular organism the possibilities of variation are almost infinite, but as soon as evolution along any line begins, these possibilities are restricted, and become more and more so the more highly specialized the animal is; in short, the potential variation of an organism becomes less and less as specialization advances. Furthermore, under the influence of natural selection in each generation the individuals which tend to vary in the same direction will survive, while at the same time, as already pointed out, their capacity for variation becomes more and more restricted. The consequence of this will be that the more highly specialized any stock becomes the more the individuals composing it will come to resemble one another, until at length the same results as arise from close interbreeding, viz, weakening of the stock, and, finally, extinction, may follow.

Abel, in discussing the whole subject of extinction (1904.1, pp. 739–748), favors the hypothesis of the reduction of variability as one of the causes of extinction. He observes:

> Even though it will never be possible to unravel the ultimate causes of the extinction of species, it remains certain that not only external factors but the internal organization as well are to be considered in seeking the ultimate explanation. In most cases probably an excessive, one-sided specialization in combination with a reduction of variability has led to extinction. * * * Much difficulty has arisen from the confusion of the conception of senility of certain types with that of predestined duration or of the restriction of vital energy. Because certain series of extinct animals show signs of degeneration in the last stages of their history it was assumed [for example, by Brocchi] that every species, genus, family, etc., has a prescribed limit of existence, at the end of which the species decays and dies like the individual. The opponents of the hypothesis of progressive reduction of variability pointed to the existence of persistent types from the Cambrian to the present time. Whenever we keep in mind the conception of progressive reduction of variability such facts can be interpreted in a new light. Then it is seen that one-sided specialization and associated with it the reduction of variability cause a weakening of the entire constitution and invite extinction, while, on the other hand, conservative, persistent types may live through long periods of time. Furthermore, a review of the past shows that rapidly and richly varying groups die out sooner than slowly developing series.
>
> Darwin, Haeckel, and Weismann are upholders of the theory of unlimited variability. Haeckel admits that groups that are becoming extinct produce no new varieties. As a matter of fact, a large number of highly specialized forms have died out as the result of their inability to vary sufficiently, and as Wallace [1889.1] pointed out, the possibility of successful adaptation stands in direct relation to the number of favorable variations. However, the number of variations declines as specialization progresses, and it is this restriction of the limits of variation which makes us better able to determine relationships of forms near the end of their phylogenetic evolution than in the early stages where variations and mutations are more numerous and the species, which arise in an explosive manner, differ greatly from one another. * * * But not only hypertrophy of the entire body but hypertrophy of certain organs to a great extent also appears toward the end of phylogenetic series. Very often this may furnish cause for extinction. The question of excessive specialization at the end of a phylogenetic series leads to a consideration of the problem of degeneration or "paracme" [Haeckel, 1906.1, pp. 366, 383].

SPECIAL FEATURES OF THE EXTINCTION OF THE TITANOTHERES

In considering the possible causes of the extinction of the titanotheres and comparing those operating in the case of other mammals we may now sum up the observations which have been more or less fully commented upon in this chapter.

Increase of individual size.—The general uniform increase in individual size in the titanotheres in both the Oligocene and the Eocene epochs indicates that all conditions of life were then remarkably favorable. This is apparently demonstrated by the fact that with one exception the animals in every line of ascent, both Eocene and Oligocene, steadily increased in size. The single exception is the diminutive, supposed aquatic species *Metarhinus fluviatilis* of the basal upper

Eocene. The practically universal increase betokens in general the long continuance of favorable conditions of life, which seem to have affected all lines of descent.

Extinction at the period of maximum growth and size.—Almost without exception extinction in each of the lines of Eocene and Oligocene titanotheres was not preceded by dwarfing but occurred at the period of greatest prosperity and after the completion of a long period of unchecked development. Large size in itself is not a cause of extinction.

No numerical increase apparent.—Although our data are far from sufficiently complete to warrant a positive statement, we may say that there is at present no evidence of a marked general increase of numbers among the titanotheres such as we observe among other mammalian phyla—the oreodonts and the horses in certain beds, for example.

Adequate brain capacity.—Although the brain capacity of the titanotheres is not so large relatively as that of some existing mammals of similar size, the brain steadily increases in size as we pass from the Eocene to the Oligocene forms, and there is not sufficient ground to consider lack of intelligence as a cause of the sudden extinction of these animals.

Molar tooth structure in relation to longevity.—The direct correlation between the longevity and the fertility of the quadrupeds with hypsodontism (elongation of the crowns of the grinding teeth), enabling animals to live a great number of years, has been pointed out. Horses, with their long-crowned teeth, live for 25 years and, foaling every year, would produce 22 young; elephants, with their long-crowned teeth, live 90 years and produce several pairs of young. In contrast, such a titanothere as the Eocene *Palaeosyops*, with its short-crowned teeth, would live for a comparatively short period and would produce comparatively few young. Theoretically this principle might be one of the means of explaining the early dying out of the broad-skulled genus *Palaeosyops*, with its short-crowned molar teeth, were it not for the contradictory fact that *Manteoceras*, also with short-crowned molars, survived, whereas *Telmatherium*, with relatively long-crowned teeth, apparently became extinct.

Inadaptation of the grinding teeth.—We have shown that the upper Oligocene titanotheres were apparently making an effort to evolve a hypsodont tooth pattern by the elongation of the outer side (ectoloph) of the superior grinding teeth, but that apparently this effort was futile because of the complete separation of the protocone on the inner side of the tooth. Such a tooth is half hypsodont, half brachyodont, and is obviously inadaptive.

Apparently the titanotheres reached a cul de sac of evolution in their grinding teeth, and this, on the whole, seems to be the single set of organs in which the titanotheres probably failed to meet the new conditions of food on the Great Plains. We conclude from the extinction of the large-toothed *Menodus ingens* that it was not the size of the teeth but the mechanical pattern that was unadapted to the new environment; no further mechanical progress or perfection was possible, hence the cul de sac.

It is noteworthy that every family of mammals that experimented with teeth of this type (Anoplotheriidae, Anthracotheriidae, Chalicotheriidae) became extinct sooner or later in Tertiary time.

There is strong collateral evidence for Kovalevsky's theory that the influence of the teeth is a chief factor in extinction. The only type of mammal with bunoselenodont grinding teeth which survived through Miocene time was the chalicothere, probably because it became a forest-frequenting animal.

A combination of other causes does not preclude the probability that the inadaptation of the teeth was the chief or leading cause of the numerical reduction and finally of the extinction of the titanotheres.

CONCLUSIONS REGARDING THE THEORY OF NATURAL SELECTION OF DARWIN AND WALLACE

Negative evidence as to minute variation.—The foregoing survey of the evolution of the titanotheres and of the causes of extinction among mammals in past and present time does not appear to support the distinctive feature of Darwin's theory that minute heritable variations (that is, mutations) have sufficient survival value to guide the course of evolution. The chief exceptions to this statement are seen in the very high survival value of immunity to disease and, conversely, the high eliminating value of nonimmunity, which may possibly appear in some individuals as sudden variations or saltations.

Degrees of survival value; utility of organs.—Paleontology and mammalian zoology now afford positive evidence that the structural and functional inadaptation of certain organs to environment has been a primary cause of extinction at all times but chiefly during stress of changes in climate, in physical conditions, and in life environment. We observe that certain combinations of mechanical structure and function have finally proved fatal to all mammals possessing them. Thus we are able to state positively that certain single organs of the bony or dental mechanism have had distinct survival or elimination value.

Combination of organs and adaptability.—There is evidence that in past and present time those animals tend to survive which present the highest adaptive combination of favorable characters, of fully formed organs, the highest adaptability in structure or in habit, the highest potentiality of further evolution toward new favorable types of habit and of structure.

Survival value of single organs.—There is evidence that in phyletic, generic, and family selection, not

only such general adaptive or inadaptive combinations occur as those above cited, but single adaptive or inadaptive organs, such as the brain, the limbs, the feet, the teeth, the horns, have in course of time been contributory causes of survival or of elimination, partly because of direct adaptation or inadaptation, partly because of indirect inadaptation to changes of environment and of life environment.

Positive evidence.—Simultaneously over large areas of the world extreme specialization, the development of certain dominant characters, has been followed by extinction: large-brained have replaced small-brained phyla; certain types of limb and foot structure have proved fatal to their possessors. This is direct confirmation of the broad original form of the Darwin-Wallace hypothesis so far as it applies to individuals as a whole and to the groups of individuals known as varieties, races, species.

Negative evidence.—This evidence, however, does not touch the queston of the survival value of "minute variations in structure, be they ever so slight," to use the Darwin-Wallace language. It does not appear that paleontology or mammalian zoology can give the final answer to this special feature of the Darwin-Wallace hypothesis. It is, however, here pointed out under the heading "Modes and factors of evolution" (sec. 1 of this chapter) that certain fluctuations of proportion may have distinct survival value and tend to be accumulated through natural selection.

Minute biocharacters and survival.—It is impossible to determine from paleontology how early in the rise of a new character, such as the minute rectigradations on the grinding teeth, there may be a sufficient survival value, or utility, to bring the character under the action of selection; opinions differ on this point; we can neither prove nor disprove the survival value of certain minute rectigradations. Our own opinion, incapable as yet of demonstration, is that natural selection may influence the transformation as soon as a number of these biocharacters (either rectigradations or allometrons) reach such a stage of development as the "mutation of Waagen." It is not impossible that there may be natural selection in these mutation stages. Our opinion is more positive against the hypothesis that selection is the cause of these rectigradations.

General conclusions.—Our general conclusions as to the part natural selection plays on minute variations, mutations, and fluctuations are negative. It is reasonably certain that under Darwin's general law of selection each strain of individual descent is improved as a whole, but it is still uncertain, largely hypothetical, undemonstrated experimentally, how far special selection explains the adaptive evolution of minute separate organs or parts, such as the incipient cusps on the teeth (rectigradations), the incipient rudiments of the horn (rectigradations), the countless minor changes of form and proportion (allometrons). As shown in section 1 of this chapter, these biocharacters seem to be largely orthogenetic in origin and to arise quite independently of natural selection. The conclusion we have reached is that new rectigradational and proportional characters may become a cause of survival or extinction as soon as they reach a stage of survival value—as soon as they are important enough to cause the life or the death of the animal in competition with other characters.

SUMMARY OF CONCLUSIONS

The present aspects of the evidence appear to be as follows:

Intervariation selection: There is no evidence that minute individual variations, except immunity to disease, have been a cause of the origin or evolution of new characters.

Interfluctuation selection: There is considerable evidence from both paleontology and zoology that the selection of fluctuations of proportion may have been a potent factor in evolution.

Interrectigradation selection: There is no reason to believe that minute rectigradations, in their most rudimentary stages, have sufficient survival value in competition with other biocharacters to affect the life of an organism.

Interorgan selection: It is demonstrated that single structures, organs, or functions can certainly be the causes of survival or extinction, especially under conditions of stress of environment—biologic or physical.

Interindividual selection: The chief action of selection between individuals seems to be to standardize—to keep every individual as a whole up to or above the average of adaptability of the group to which it belongs. Individuals that combine the largest number of favorable, adaptive, and adaptable characters are constantly being selected. In this process organic or coincident selection plays a large part.

Intergroup selection: By a study of local adaptive radiation of the titanotheres we have discovered many separate lines of descent in which similar biocharacters were evolving at different rates. There has been more or less competition between these groups, varieties, races, and species. Here we observe especially the survival of the unspecialized forms and the extinction of the extremely specialized forms.

Intergeneric, subfamily, family, and superfamily selection: The principle just stated applies to selection in relation to the survival or elimination of subfamily, family, and superfamily divisions.

To sum up: Natural selection appears to be operating incessantly and positively to preserve and accumulate characters that have survival value and to eliminate all other characters. Numerical reduction within a group and even extinction may be due to a single eliminating cause or to a combination of eliminating causes.

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PLATE XLV

PLATE XLV

Ontogenesis of the Horns of Domestic Cattle

Development of the horny sheath and the osseous horn in seven stages. Drawn from preparations made by S. H. Chubb, in the collections of the American Museum of Natural History.

A, Foetal skull, approximately in the fifth month of the intrauterine growth. The future horn area is indicated by a thickening of the epidermal cells, from which arise 40 scattered hairs (first stage of the hair tuft).

B, Foetal skull approximately of the sixth or seventh month. Epidermal thickening enlarged, covered with the pointed and partly agglutinated hair tuft (beginning of the horn sheath).

C, Foetal skull of the ninth month, in which first appears the osseous horn rudiment covered with a cap of thickened epidermis and a rudiment of the horn sheath of the agglutinated hairs.

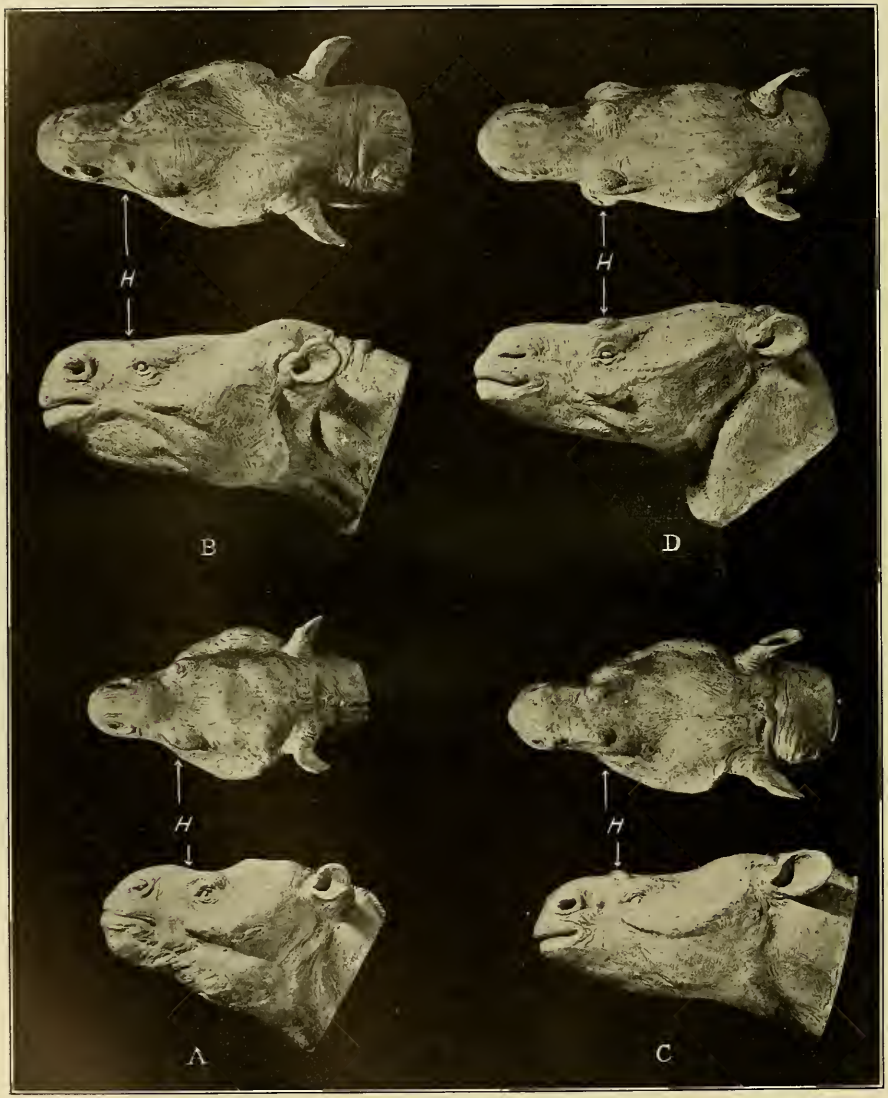
D, Skull of calf two weeks after birth, in which the osseous horn and the horn sheath are shifting back toward the occiput, through the ontogenetic allometric development of the frontals and recession of the parietals.

E, Skull of calf two months after birth, showing the allometric shifting of the small osseous horn and the horn sheath toward the occiput.

F, Yearling skull of 18 months, in which the osseous horn and the sheath are fully shifted back upon the occiput.

G, Adult skull of the ninth year, showing the completed osseous.

ONTOGENESIS OF THE HORNS OF DOMESTIC CATTLE



MODELS OF HEADS OF EOCENE TITANOTHERES, SHOWING BRACHYCEPHALY, MESATICEPHALY, AND DOLICHOCEPHALY

A, *Palaeosyops leidyi*, brachycephalic. B, *Manteoceras manteoceras*, mesaticephalic. C, *Telmatherium ultimum*, mesaticephalic. D, *Dolichorhinus hyognathus*, dolichocephalic. H, Horn swelling

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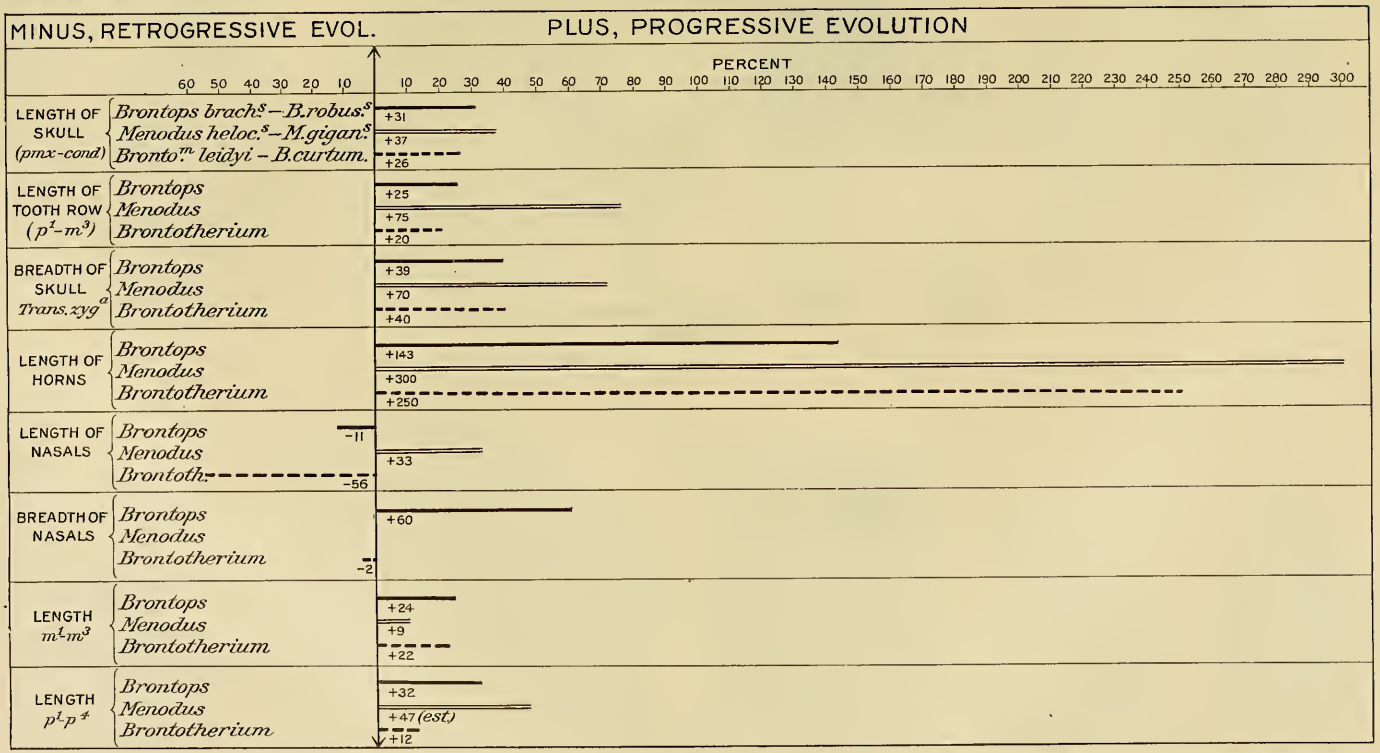
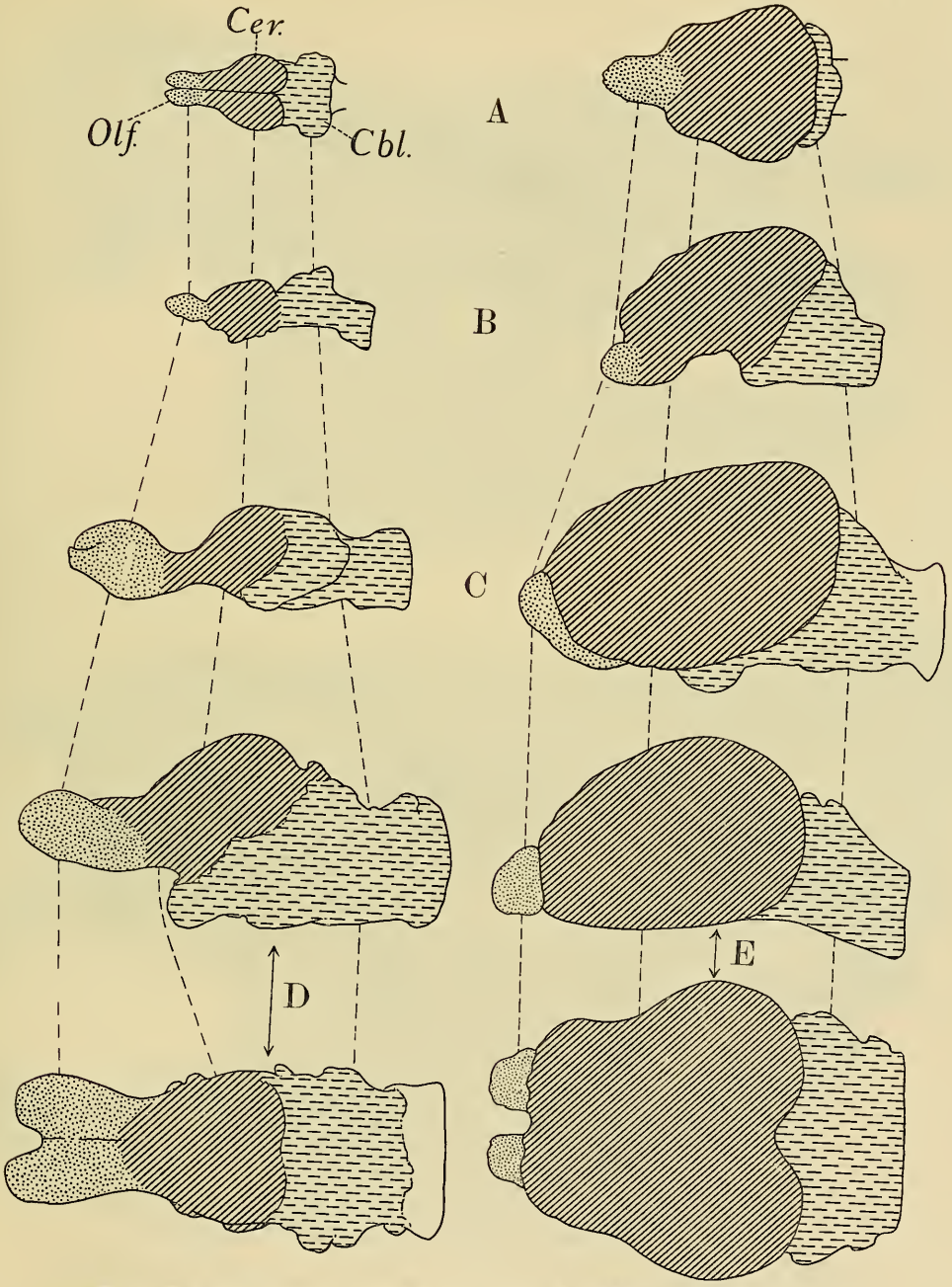


DISHARMONIC DIFFERENTIAL EVOLUTION OF CHARACTERS IN SKULLS AND TEETH OF THREE GENERA OF TITANOTHERES DURING LOWER OLIGOCENE TIME

Each genus has its distinctive increment and decrement in each character

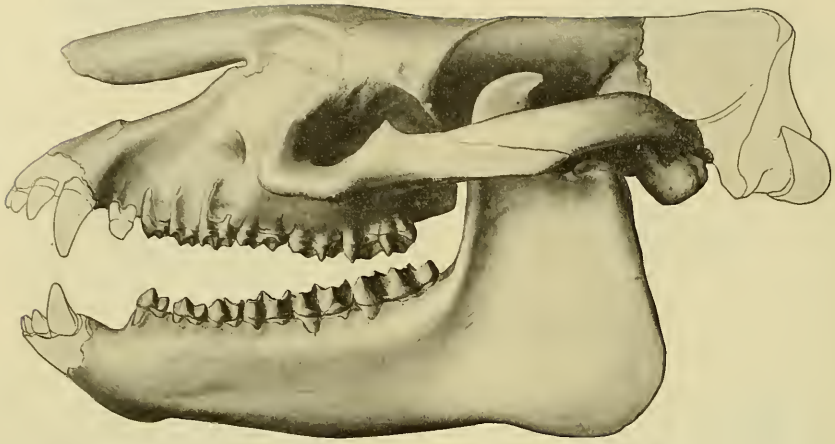
EXTINCTION OR SURVIVAL OF 23 FAMILIES OF EVEN-TOED ARTIODACTYL UNGULATES

Note the extinction of 13 families having bunodont and bunoselenodont grinding teeth, the survival of 3 bunodont families, and the expansion of 7 selenodont families



BRAIN OF EOCENE MAMMALS COMPARED WITH THAT OF MODERN AND OTHER MAMMALS

Archaic forms in left column; modernized forms in right column. Olfactory lobes represented by dots; cerebral hemispheres by black lines; cerebellum and medulla by dashes. A, *Arctocyon*, Eocene flesh eater; *Canis*, the dog, modern flesh eater. B, *Phenacodus*, Eocene primitive ungulate; *Sus*, the domestic pig. C, *Coryphodon*, Eocene ungulate; *Rhinoceros*, living rhinoceros of same size. D, *Uintatherium*, massive Eocene ungulate. E, *Menodus giganteus*, Oligocene titanothere. All over one-fourth natural size



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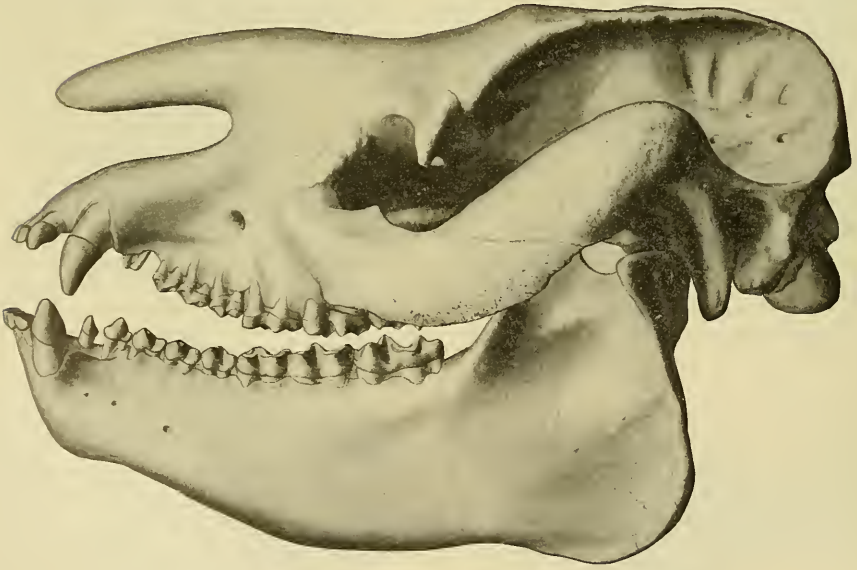
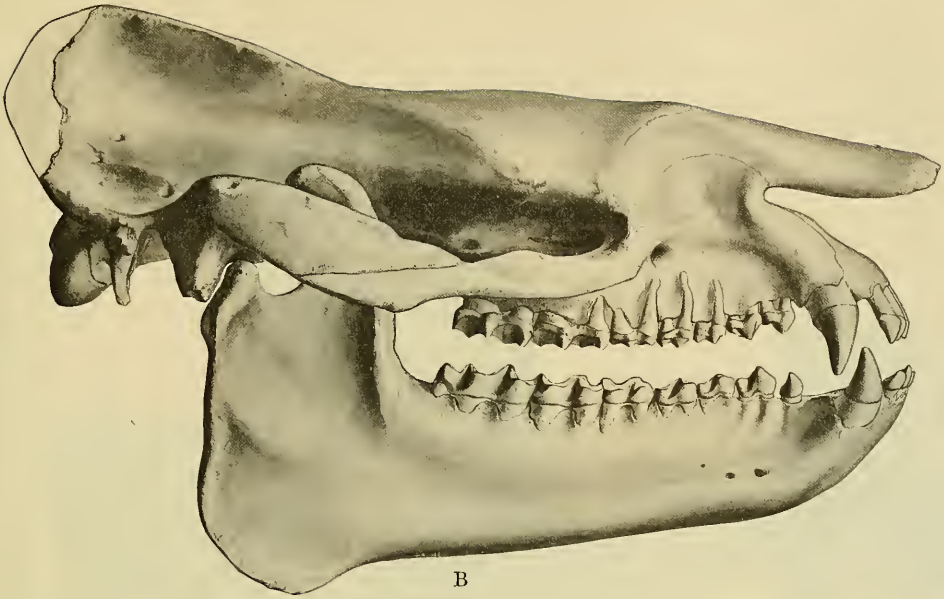


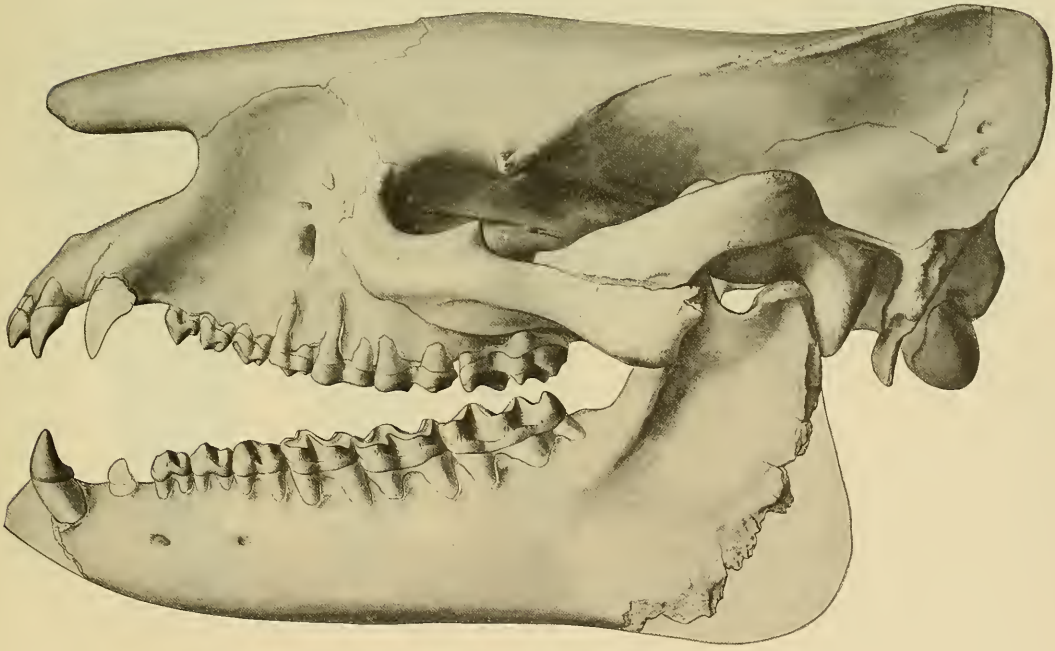
A

TYPE SKULLS OF PALAEOSYOPS LEIDYI AND MESATIRHINUS PETERSONI

A, *Palaeosyops leidyi*, type (Am. Mus. 1544), Bridger Basin, Wyo., level Bridger C or D. B, *Mesatirhinus petersoni*, type skull (Am. Mus. 12184), Cattail Springs, Bridger Basin, Wyo., level Bridger D 3; lower jaw (Am. Mus. 1512), Laclede Meadows, Washakie Basin, Wyo., level Washakie A. Both one-third natural size



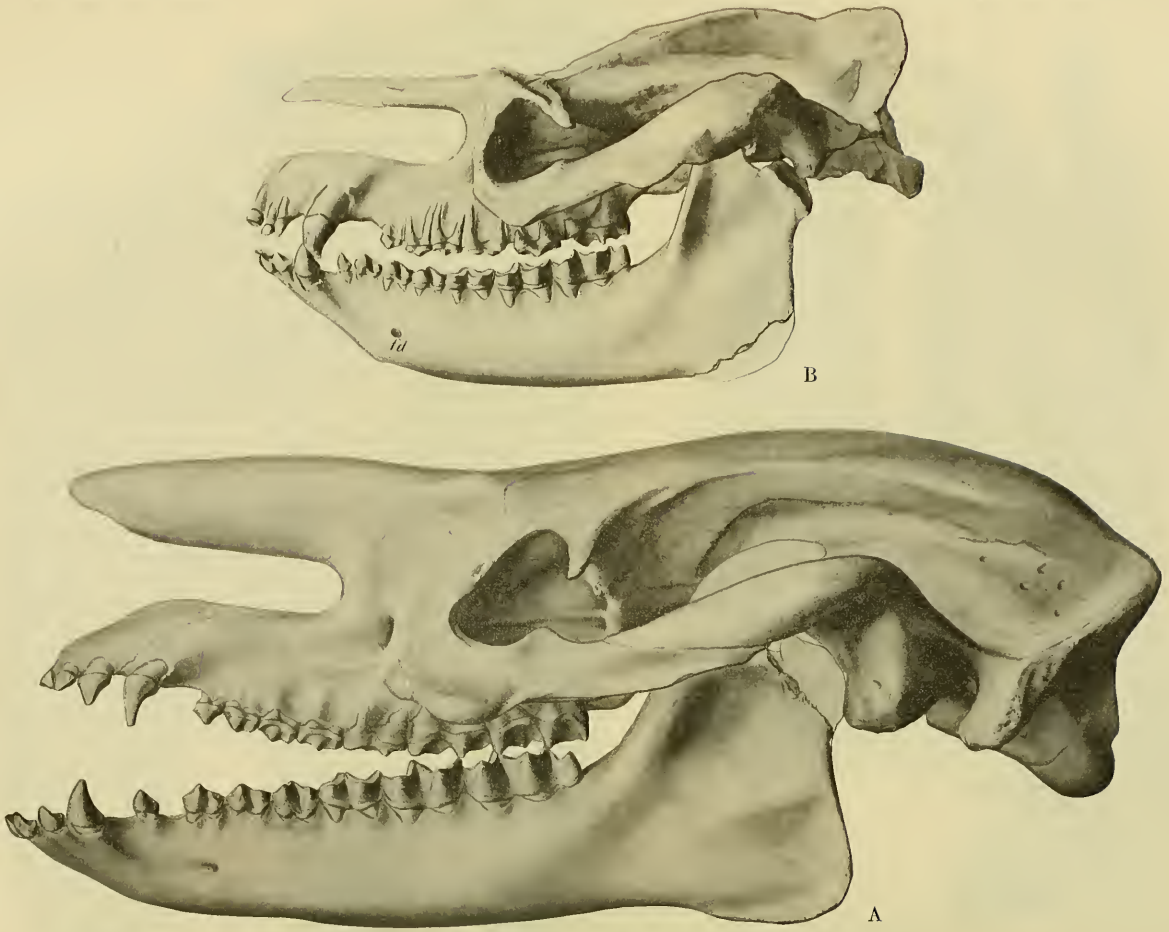
B



A

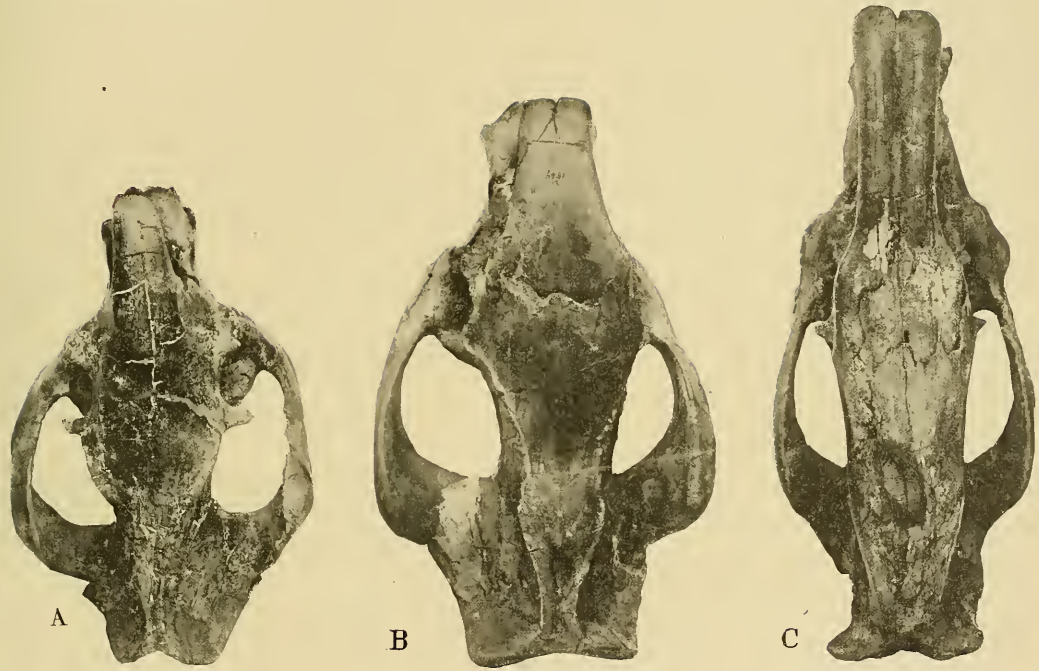
SKULLS OF TELMATHERIUM ULTIMUM AND MANTEOCERAS MANTEOCERAS

A, *Telmatherium ultimum*, type (Am. Mus. 2060), Uinta Basin, Utah, level Uinta C. B, *Manteoceras manteoceras* (Am. Mus. 2353), south of Haystack Mountain, Washakie Basin, Wyo., level Washakie A(?), canines and incisors partly restored from Am. Mus. 1566. Both one-third natural size



SKULLS OF DOLICHORHINUS HYOGNATHUS AND METARHINUS FLUVIATILIS

A, *Dolichorhinus hyognathus*, skull (Am. Mus. 1851, type of *D. cornutus*), Uinta Basin, Utah, level Uinta B 2; lower jaw (Am. Mus. 1856), Uinta Basin, level Uinta B 2. B, *Metarhinus fluviatilis*, type skull (Am. Mus. 1500), Uinta Basin, level Uinta B 1; lower jaw (Am. Mus. 2059), Uinta Basin, level Uinta B 1. Both one-third natural size



SKULL FORM IN EOCENE TITANOTHERES

A, Brachycephalic type, *Palaeosyops leidyi* (Am. Mus. 1516). B, Mesaticephalic type, *Manteoceras manteoceras* (Am. Mus. 1569). C, Dolichocephalic type, *Dolichorhinus hyognathus* (Am. Mus. 1851)

PLATE LIV

PLATE LIV

Upper and Lower Grinding Teeth of the Lower Eocene Titanotheres, Lambdotherium and Eotitanops

Drawings by E. S. Christman. Natural size. (See pp. 279, 281)

A, *Lambdotherium popoagicum* (Am. Mus. 2688), Huerfano Basin, Colo., upper fourth premolar and molars.

B, *L. popoagicum* (Am. Mus. 4864 and 4880), m^2, upper premolars and molars.

C, *L. primaevum*, type (Amherst Mus. 254), Buffalo Basin, Wyo., upper molars.

D, The same, lower molars.

E^1, *L. popoagicum* (Am. Mus. 2989), Wind River Valley, Wyo., incomplete lower dentition in jaw fragment, external view. Pm_2 in this view is restored from Am. Mus. 4863, a somewhat larger animal.

E^2, The same, internal view.

F, *Eotitanops gregoryi*, type (Am. Mus. 14889), Alkali Creek, Buck Spring, Wind River Basin, Wyo., upper level of "Big Red Pocket," 100 feet above heavy red stratum, level Wind River B ("Lost Cabin"), second and third left upper molars.

G, The same, right lower premolar-molar series; drawing reversed.

H^1, *E. borealis*, type (Am. Mus. 4892), Wind River Valley, Wyo., Wind River formation, level undetermined, right upper cheek teeth.

H^2, The same, outer side of p^4 and m^1.

I^1, *E. borealis* (Am. Mus. 14887), Dry Muddy Creek 12 miles above mouth, Wind River Basin, Wyo., Wind River formation, level undetermined, left upper premolar-molar series.

I^2, The same, outer side view of p^1–p^4.

J, *E. princeps*, type (Am. Mus. 296), Wind River Basin, Wyo., Wind River formation, level undetermined, left lower grinding teeth, crown view; drawing reversed.

UPPER AND LOWER GRINDING TEETH OF LAMBDOTHERIUM AND EOTITANOPS

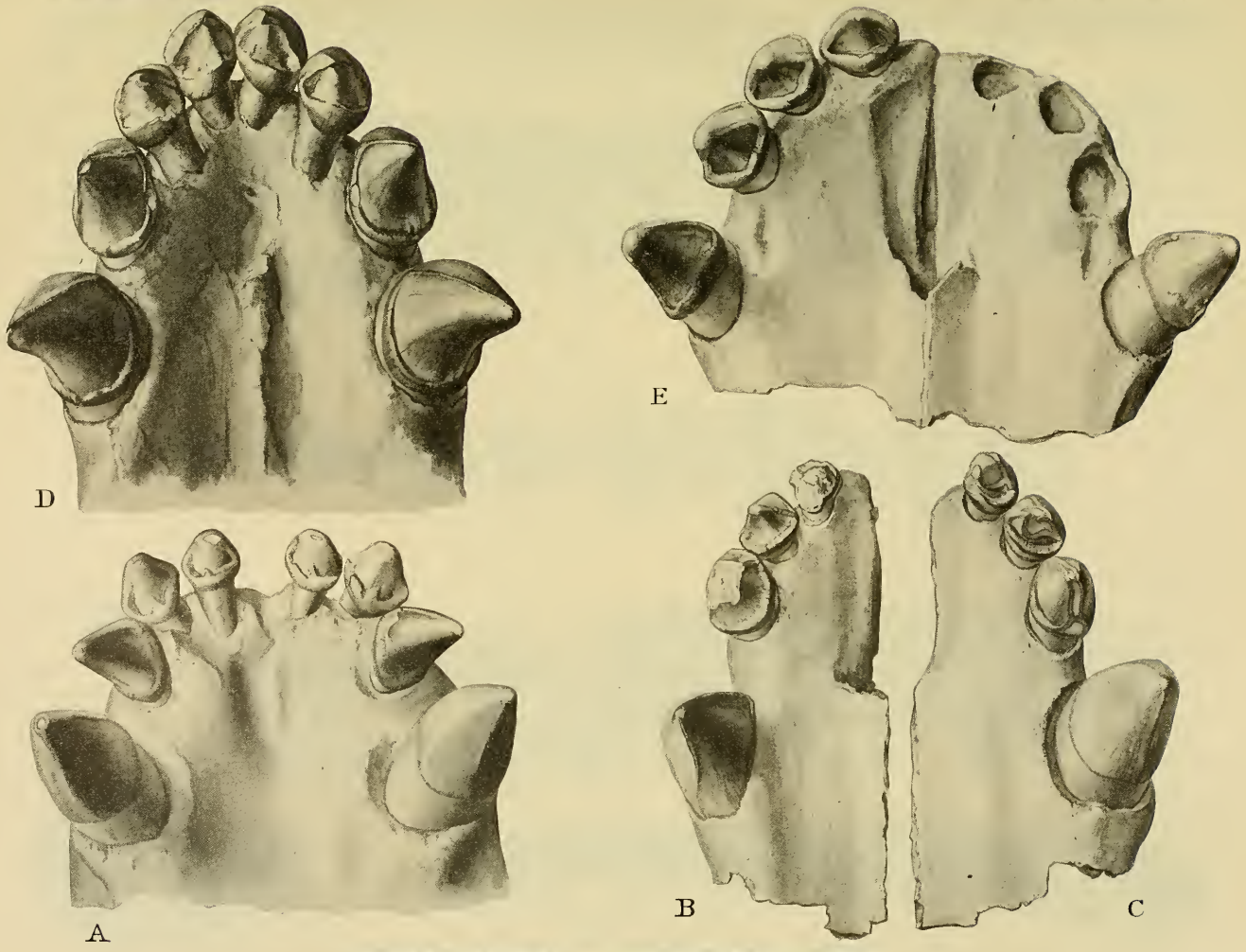
PLATE LV

PLATE LV

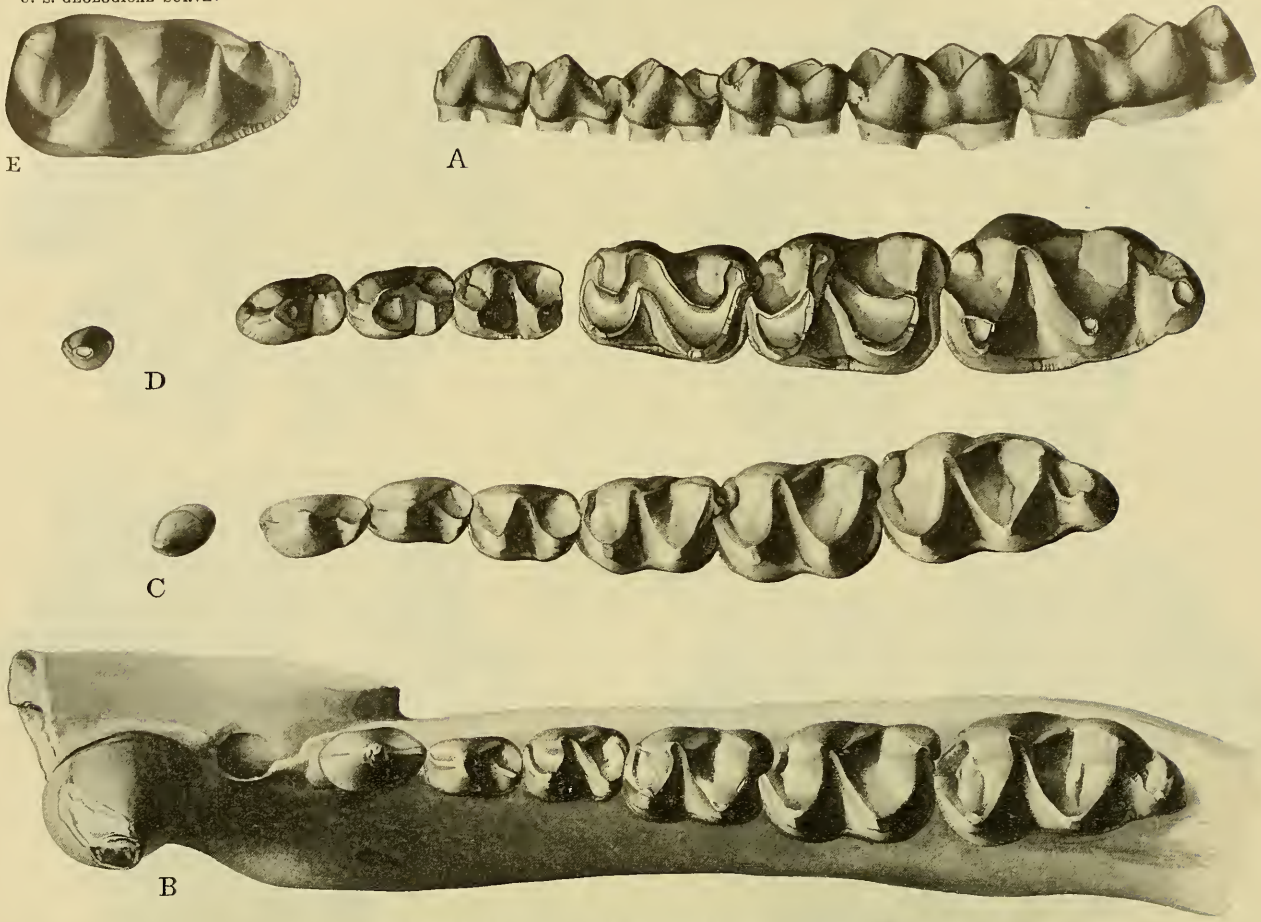
Comparison of Incisors and Canines in Eocene Titanotheres from the Upper Levels of Bridger Basin and the Lower Levels of Washakie Basin

Drawings by E. S. Christman. Natural size. (See p. 298)

A, *Palaeosyops* aff. *P. robustus* (Am. Mus. 1584), Bridger Basin, Wyo.
B, *Telmatherium cultridens* (Princeton Mus. 10027), Sage Creek Spring, Bridger Basin, Wyo.
C, *Manteoceras manteoceras* (Am. Mus. 12683), Sage Creek Spring, Bridger Basin, Wyo.
D, *Telmatherium ultimum*, paratype (Am. Mus. 2004), White River, Utah, premaxillary region crushed laterally.
E, *Dolichorhinus hyognathus* (Am. Mus. 13164), Washakie Basin, Wyo., Haystack Mountain, 10 feet above pink stratum, level Washakie B.



COMPARISON OF INCISORS AND CANINES IN EOCENE TITANOTHERES



LOWER GRINDING TEETH OF LIMNOHYOPS AND PALAEOSYOPS

Illustrating several stages in the evolution of the premolars. Drawings by E. S. Christman. Natural size. A, *Palaeosyops longirostris*, type (Princeton Mus. 10275), level Bridger B(?), p_3–m_3. B, *P. paludosus*, neotype (Am. Mus. 11680), Little Dry Creek, Bridger Basin, Wyo., level Bridger B 1, c–m_3. C, *Limnohyops priscus* (Am. Mus. 11688), Grizzly Buttes, Bridger Basin, Wyo., level Bridger B 2, p_1–m_3. D, *P. leidyi*, type (Am. Mus. 1544), Bridger Basin, Wyo., level Bridger C 4(?), p_1–m_3; drawing reversed. E, *P. robustus*, type (Yale Mus. 11122), level Bridger C or D, m_3; drawing reversed

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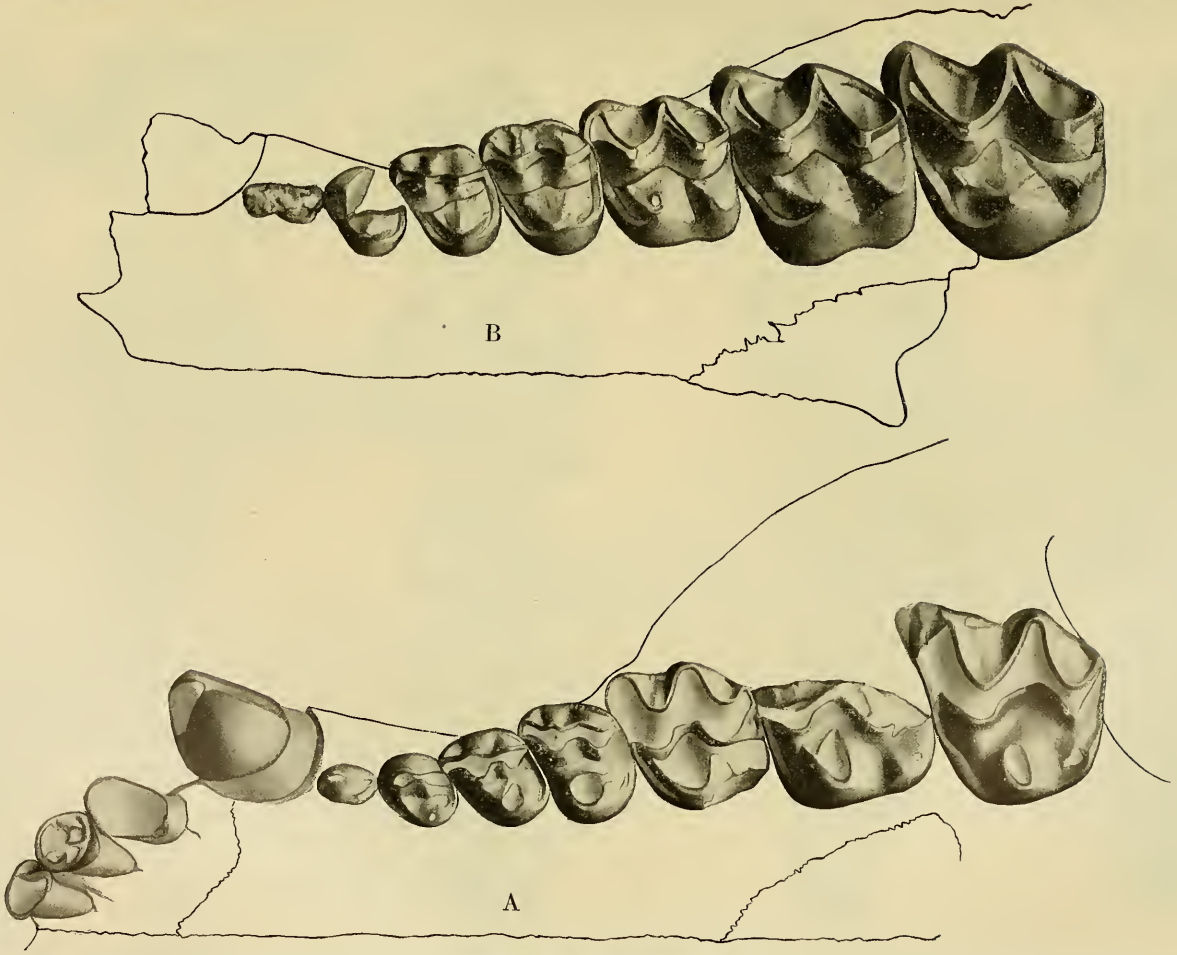
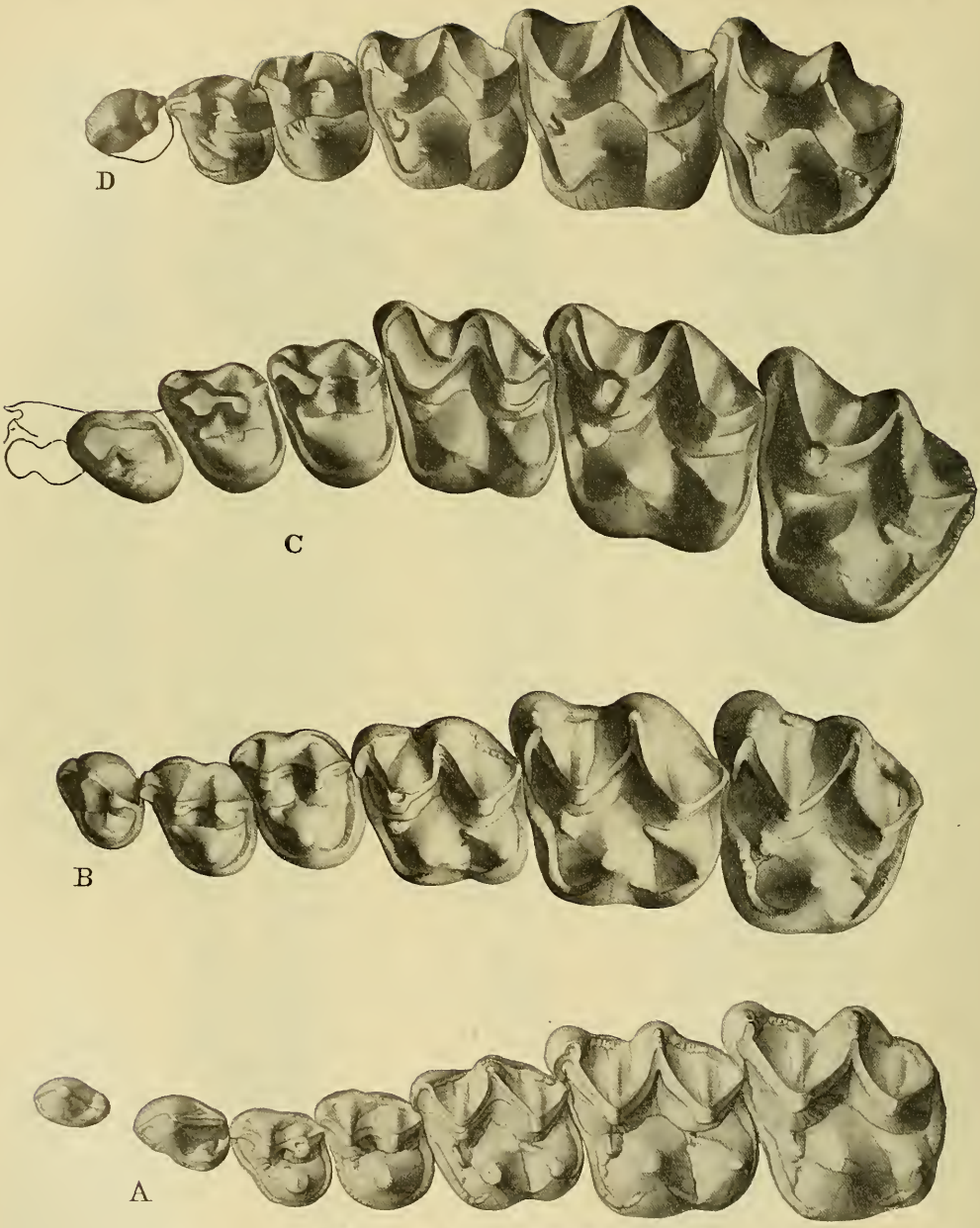


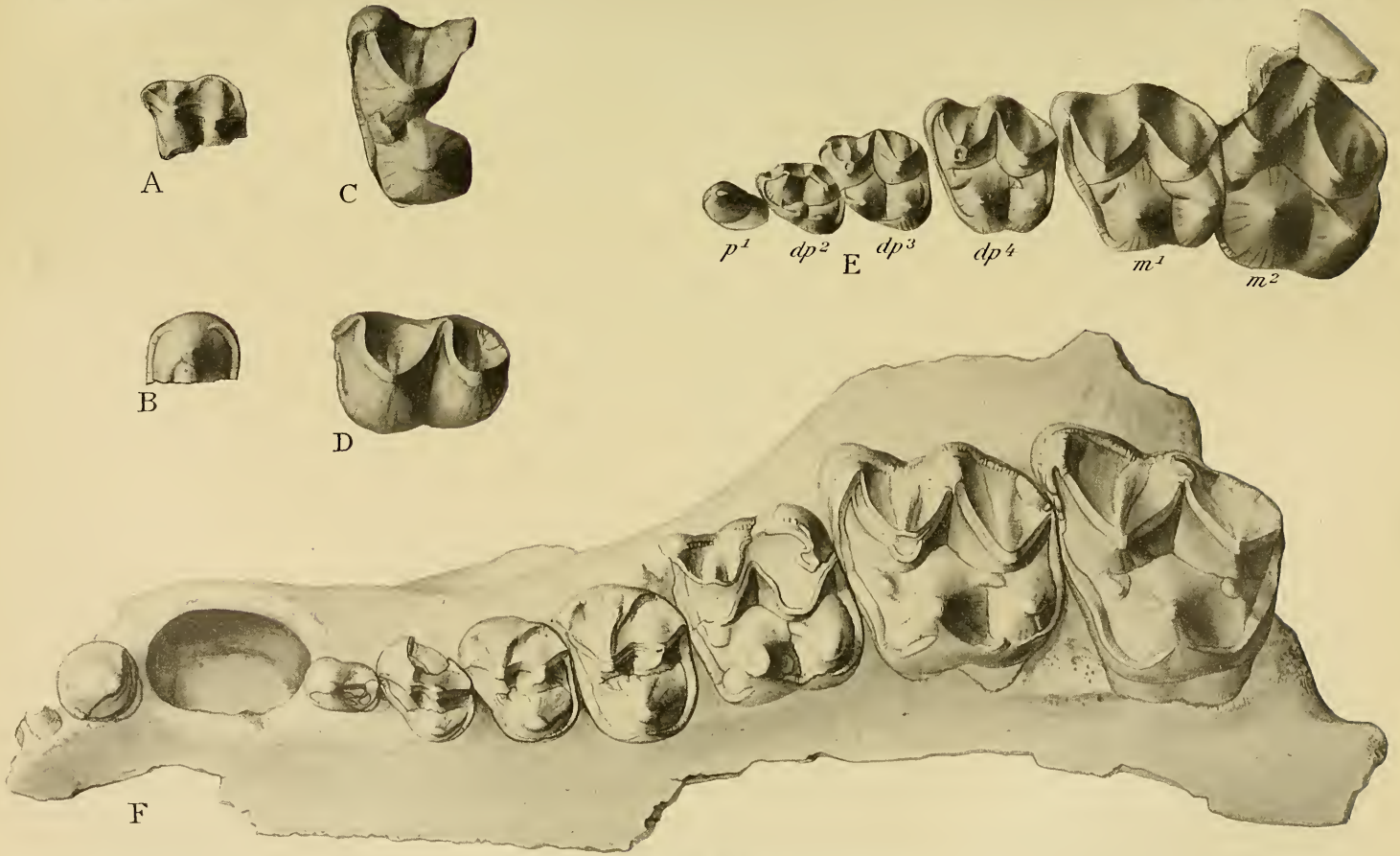
UPPER DENTITION OF LIMNOHYOPS

Drawings by E. S. Christman. (See pp. 305, 311.) Natural size. A, *Limnohyops laevidens*, type (Am. Mus. 5104), Cottonwood Creek, Bridger Basin, Wyo., level Bridger B. B, *L. laticeps*, type (Yale Mus. 11000), Bridger formation, probably level C or D. Both drawings reversed



UPPER DENTITION IN FOUR SPECIES OF PALAEOSYOPS

Illustrating successive stages in the evolution of the premolars. (See p. 314.) Drawings by E. S. Christman. Natural size. A, *Palaeosyops paludosus* (Am. Mus. 13032), 5 miles south of Granger, Wyo., level Bridger B 1, p^1–m^3. B, *P. major* (Am. Mus. 12182), middle of Cottonwood Creek, Bridger Basin, Wyo., level Bridger B 3, p^2–m^3, drawing reversed. C, *P. robustus*, type (Yale Mus. 11122), part of upper Bridger formation, probably level C or D, p^2–m^3, drawing reversed. D, *Palaeosyops* sp. (Am. Mus. 2361), south of Haystack Mountain, Washakie Basin, Wyo., level Washakie A, p^2–m^3



UPPER DENTITION IN THREE SPECIES OF PALAEOSYOPS

Drawings by E. S. Christman. (See pp. 319–335.) Natural size. A, B, and C, from Bridger B(?), are cotypes of *Palaeosyops paludosus*: A, Nat. Mus. 762, p^4 l; B, Nat. Mus. 762, p^4 r; C, Nat. Mus. 758, m^2 l. D, *P. paludosus*, lectotype (Nat. Mus. 759?), level Bridger B(?), m_1 r. E, *P. leidyi* (Am. Mus. 1565), Bridger Basin, Wyo., Bridger formation, level unknown, dp^2–dp^4, m^1, m^2, p^1. F, *P. grangeri*, type (Am. Mus. 12189), Twin Buttes, Bridger Basin, Wyo., 200 feet below red stratum, level Bridger C 1, i^3–m^3, drawing reversed

PLATE LX

PLATE LX

Upper Dentition of Limnohyops and Palaeosyops

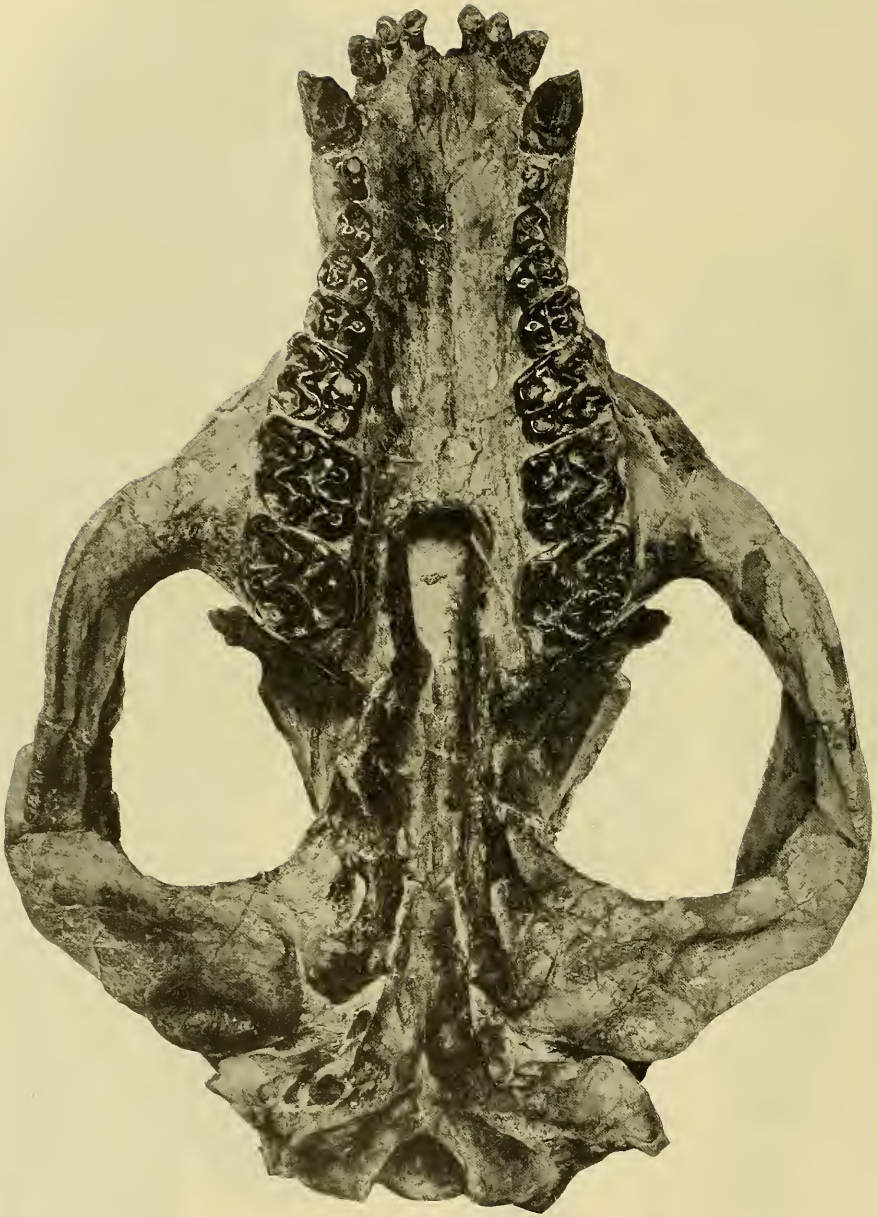
Illustrating three stages in the evolution of the premolars. (See pp. 306–336.) Drawings by E. S. Christman. Natural size

A, *Limnohyops priscus*, type (Am. Mus. 11687), Grizzly Buttes West, Bridger Basin, Wyo., level Bridger B 2; p^1–m^3. In this species the second, third, and fourth premolars are in a relatively low stage of evolution.

B. *Palaeosyops leidyi*, type (Am. Mus. 1544), Bridger Basin, Wyo., level Bridger C 4(?), i^1–m^3. In this species the premolars are in a more advanced stage of evolution.

C, *P. copei*, type (Am. Mus. 11705), Henrys Fork, Lone Tree, Bridger Basin, Wyo., level Bridger D 3, p^1–m^3, drawing reversed. In this species the premolars are in a very advanced stage of evolution.

UPPER DENTITION OF LIMNOHYOPS AND PALAEOSYOPS

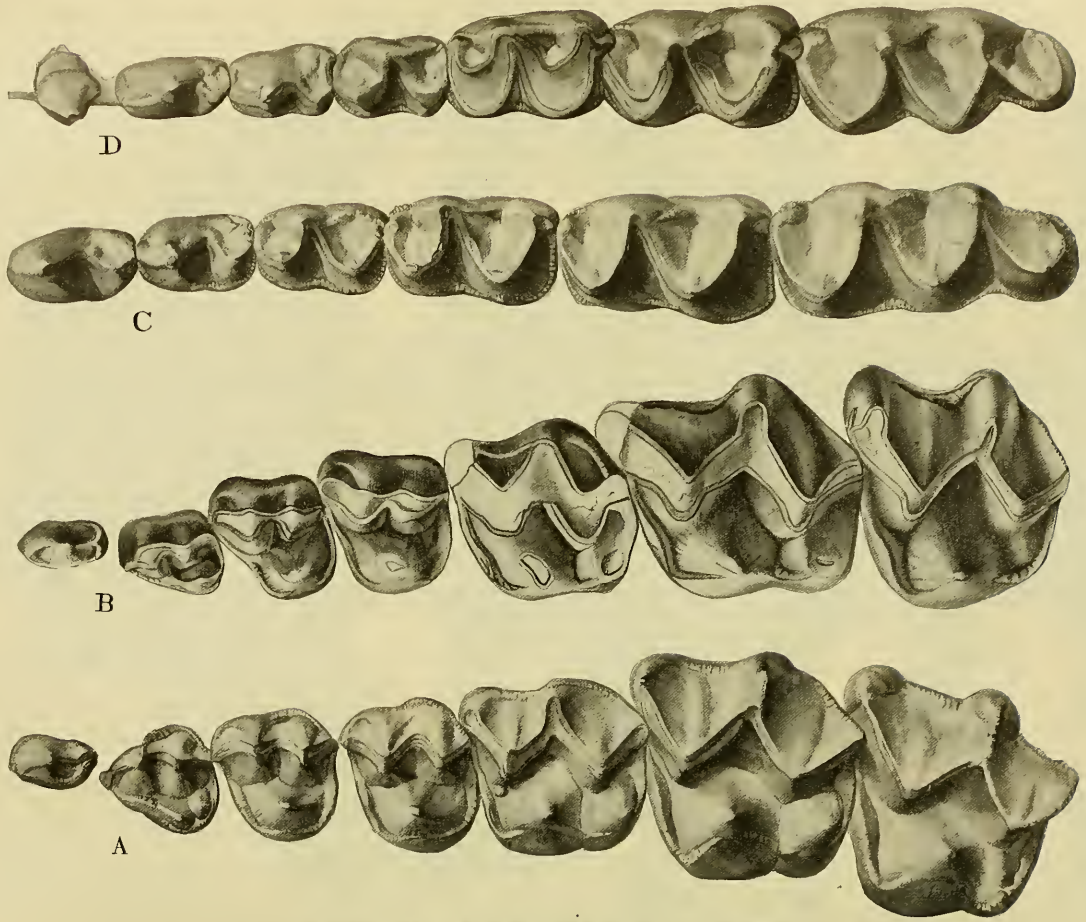


TYPE SKULL OF PALAEOSYOPS LEIDYI, PALATAL VIEW

Am. Mus. 1544, Bridger Basin, Wyo., level Bridger C 4(?). (See p. 327.) One-half natural size

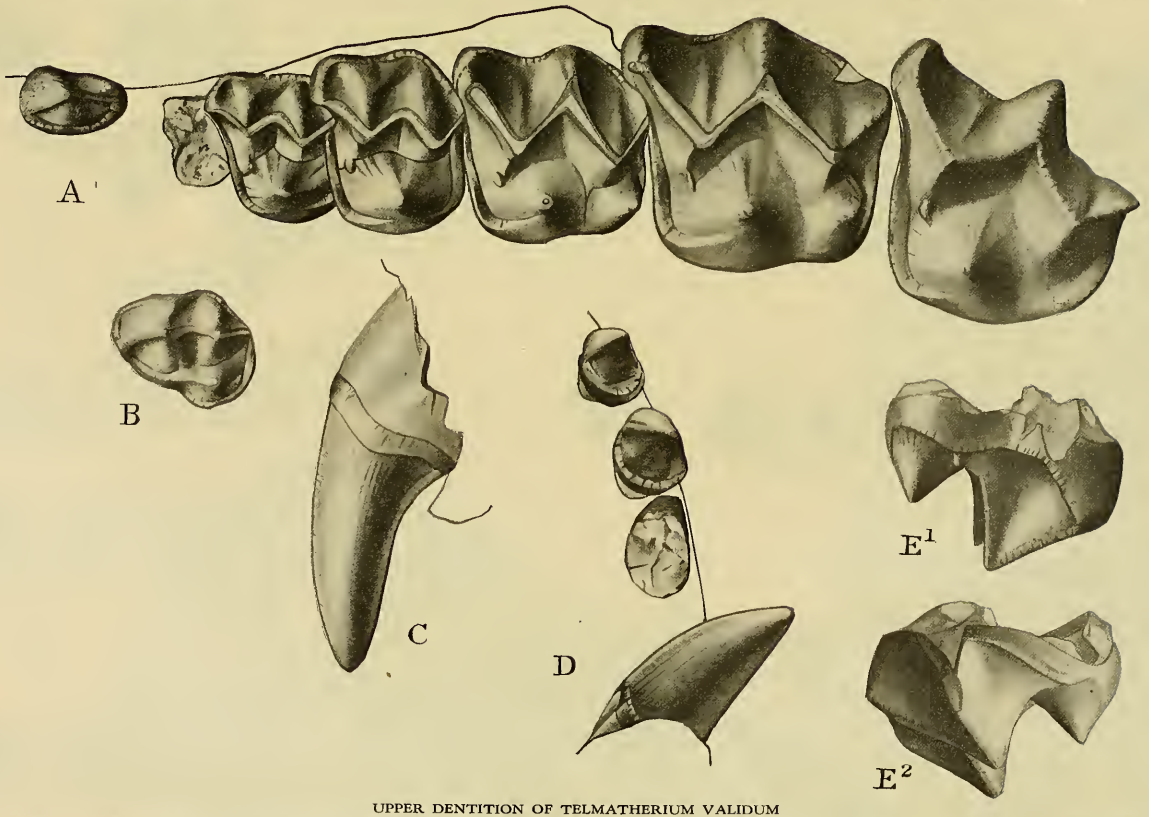
UPPER AND LOWER PREMOLARS OF LIMNOHYOPS AND PALAEOSYOPS

Drawings by E. S. Christman. (See pp. 312, 314.) Natural size. A–K, External (lateral) views of the upper premolars, showing various stages in the separation of the cingulum from the ectoloph; L–O, internal (medial) views of the lower premolars, showing various stages in the evolution of p_2, p_3. A, *Limnohyops priscus*, type (Am. Mus. 11687), Grizzly Buttes West, Bridger Basin, Wyo., level Bridger B 2, p^2–p^4, drawing reversed. B, *L. monoconus*? (Am. Mus. 5102), Cottonwood Creek, Bridger Basin, Wyo., level Bridger B, p^2–p^4, drawing reversed. C, *L. laticeps*, type (Yale Mus. 11000), Bridger formation, level?, p^3, p^4, drawing reversed. D, *Palaeosyops major*, neotype (Am. Mus. 12182), middle of Cottonwood Creek, Bridger Basin, Wyo., level Bridger B 3, p^2–p^4, drawing reversed. E, *P. paludosus*, one of the cotypes (Nat. Mus. 762), level Bridger B(?) 1–2, p^4. F, *Palaeosyops* sp. (Am. Mus. 2361), south of Haystack Mountain, Washakie Basin, Wyo., level Washakie A, p^2–p^4. G, *P. major* (Am. Mus. 12182, same as D), p^4, drawing reversed. H, *P. robustus* (Am. Mus. 1558), Twin Buttes, Bridger Basin, Wyo., level Bridger C or D, p^4, drawing reversed. I, *P. leidyi* (Princeton Mus. 10009), level Bridger C or D, p^1–p^4, drawing reversed. J, *P. robustus* (Am. Mus. 1554), Henrys Fork, Bridger Basin, Wyo., level Bridger C(?) or D, p^2–p^4, drawing reversed. K, *P. grangeri*, type (Am. Mus. 12189), Twin Buttes, Bridger Basin, Wyo., 200 feet below red stratum, level Bridger C 1, p^1–p^4, drawing reversed. L, *L. priscus* (Am. Mus. 11688), Grizzly Buttes East, Bridger Basin, Wyo., level Bridger B 2, p_2–p_4, drawing reversed. M, *P. paludosus* (Am. Mus. 11680), Little Dry Creek, Bridger Basin, Wyo., level Bridger B 1, p_2–p_4, drawing reversed. N, *P. major* (Am. Mus. 12181), middle of Cottonwood Creek, Bridger Basin, Wyo., level Bridger B 3, p_2–p_4, drawing reversed. O, *P. leidyi* (Am. Mus. 12200), Henrys Fork, Lone Tree, 50 feet below white stratum, level Bridger C 1, p_2–p_4, drawing reversed



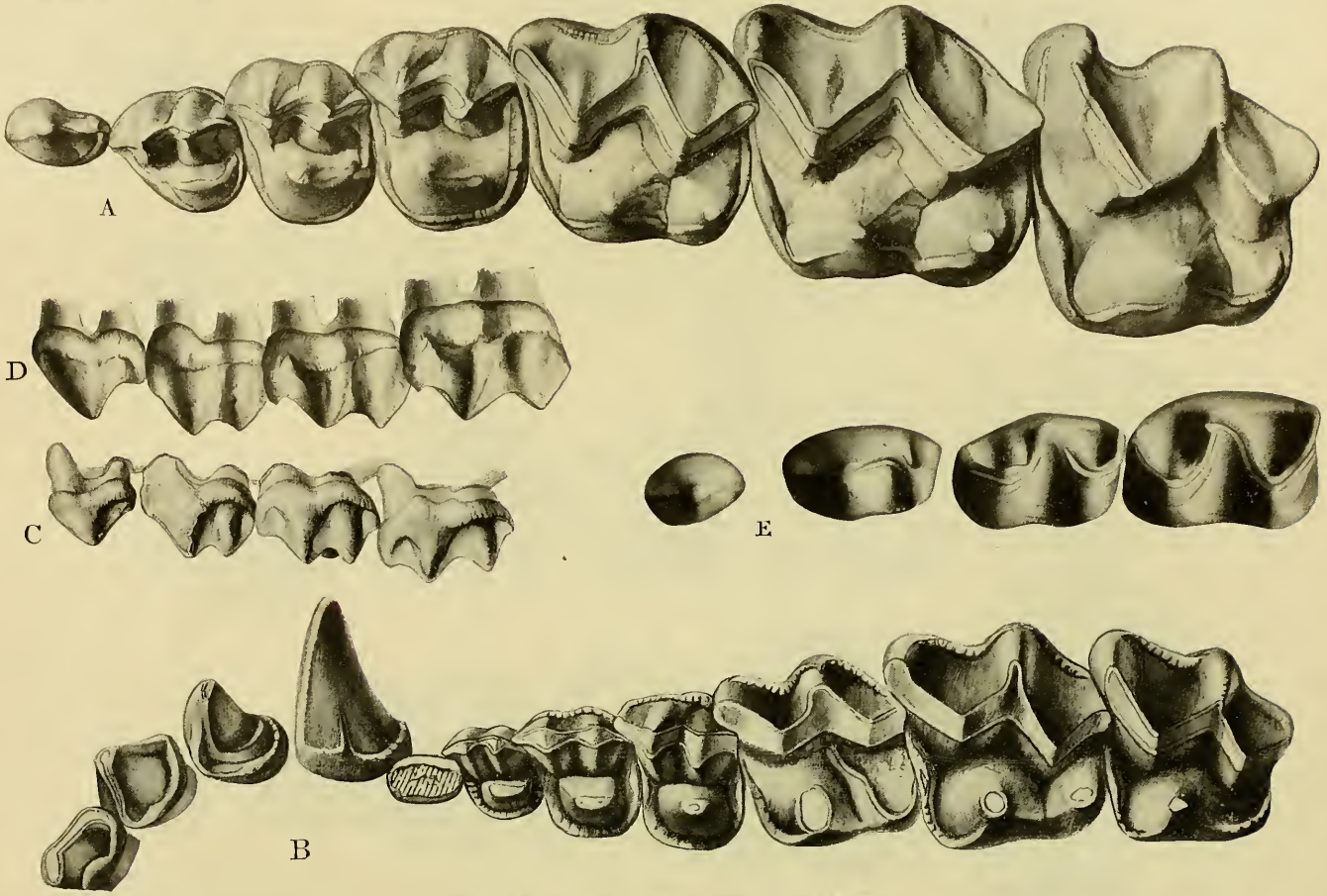
GRINDING TEETH OF TELMATHERIUM AND MANTEOCERAS

Drawings A, C, and D by E. S. Christman; B by Sidney Prentiss. (See pp. 340, 343, 368, 369.) A, *Telmatherium cultridens*, type (Princeton Mus. 10027), level Bridger D(?), p^1–m^3, natural size. B, *Manteoceras uintensis*, type (Carnegie Mus. 2388), upper premolar-molar series (after Douglass), three-quarters natural size. C, *T. cultridens*, type (Princeton Mus. 10027), level Bridger D(?), p_2–m_3, natural size. D, *M. manteoceras* (Am. Mus. 1566), Bridger Basin, Wyo., lower premolar-molar series, crown view, natural size. All drawings reversed



UPPER DENTITION OF TELMATHERIUM VALIDUM

Drawings by E. S. Christman. (See p. 344.) Natural size. Type (Yale Mus. 11120), level Bridger D(?). A, p^1–m^3, crown view; B, p^2, crown view; C, right canine, inner side; D, incisors and canine, crown view; E^1, m^3, anterior view; E^2, m^3, posterior view



DENTITION OF TELMATHERIUM AND STHENODECTES

Drawings A, C, D, E by E. S. Christman, natural size; B by Sidney Prentiss, three-fourths natural size. (See pp. 342, 355, 356.) A, *Telmatherium ultimum*, paratype (Am. Mus. 2004), White River, Utah, level Uinta C, near base, p^1–m^3, drawing reversed. B, *Sthenodectes incisivus*, type (Carnegie Mus. 2398), upper dentition (after Douglass). C, *T. cultridens*, type (Princeton Mus. 10027), level Bridger D(?), premolar ectolophs, drawing reversed. D, *T. ultimum* (Am. Mus. 2004, same as A), premolar ectolophs, drawing reversed. E, *T. altidens*, type (Am. Mus. 2025), White River, Utah, base of Uinta C, p_1–p_4, crown view, drawing reversed

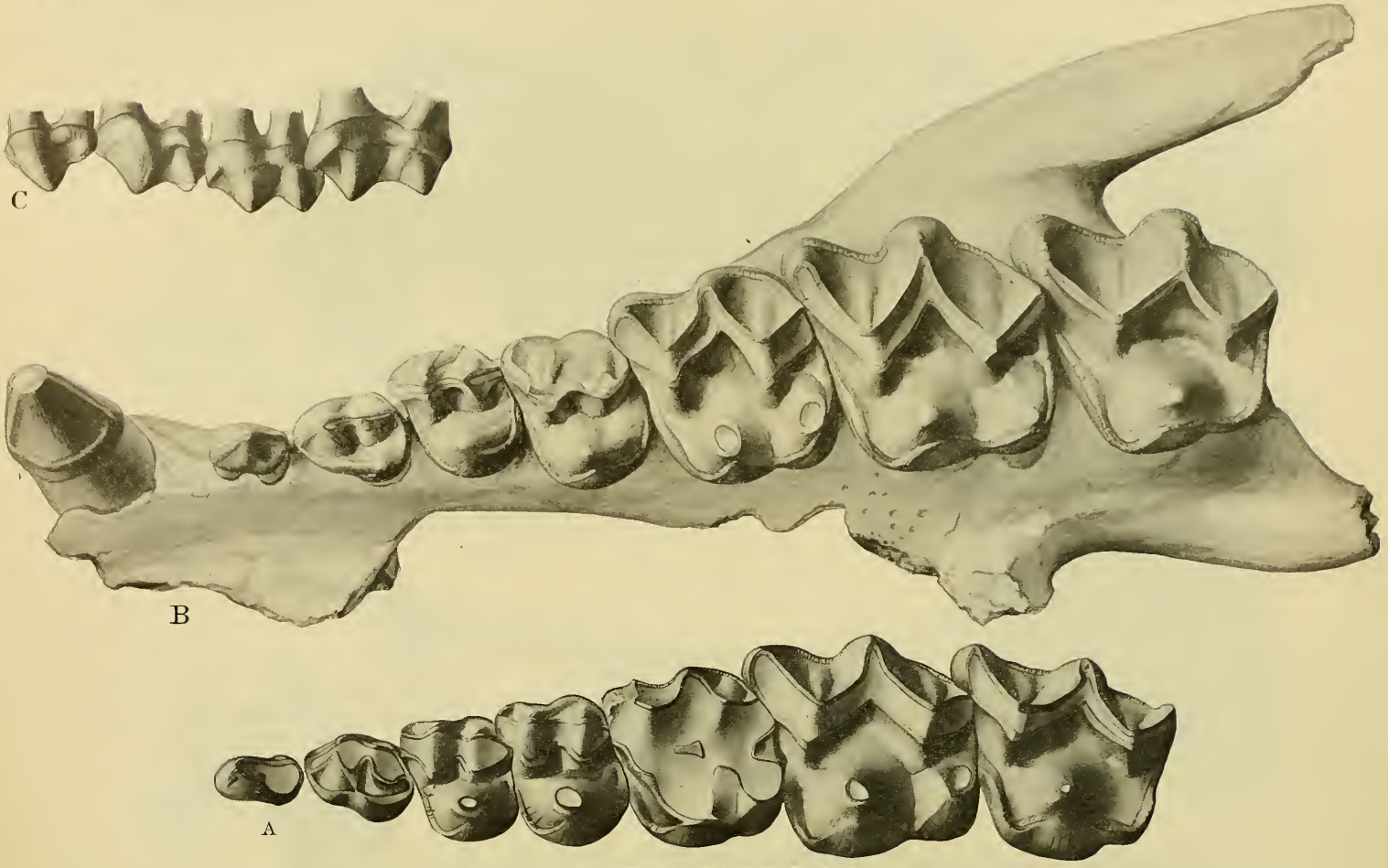
A

C

B

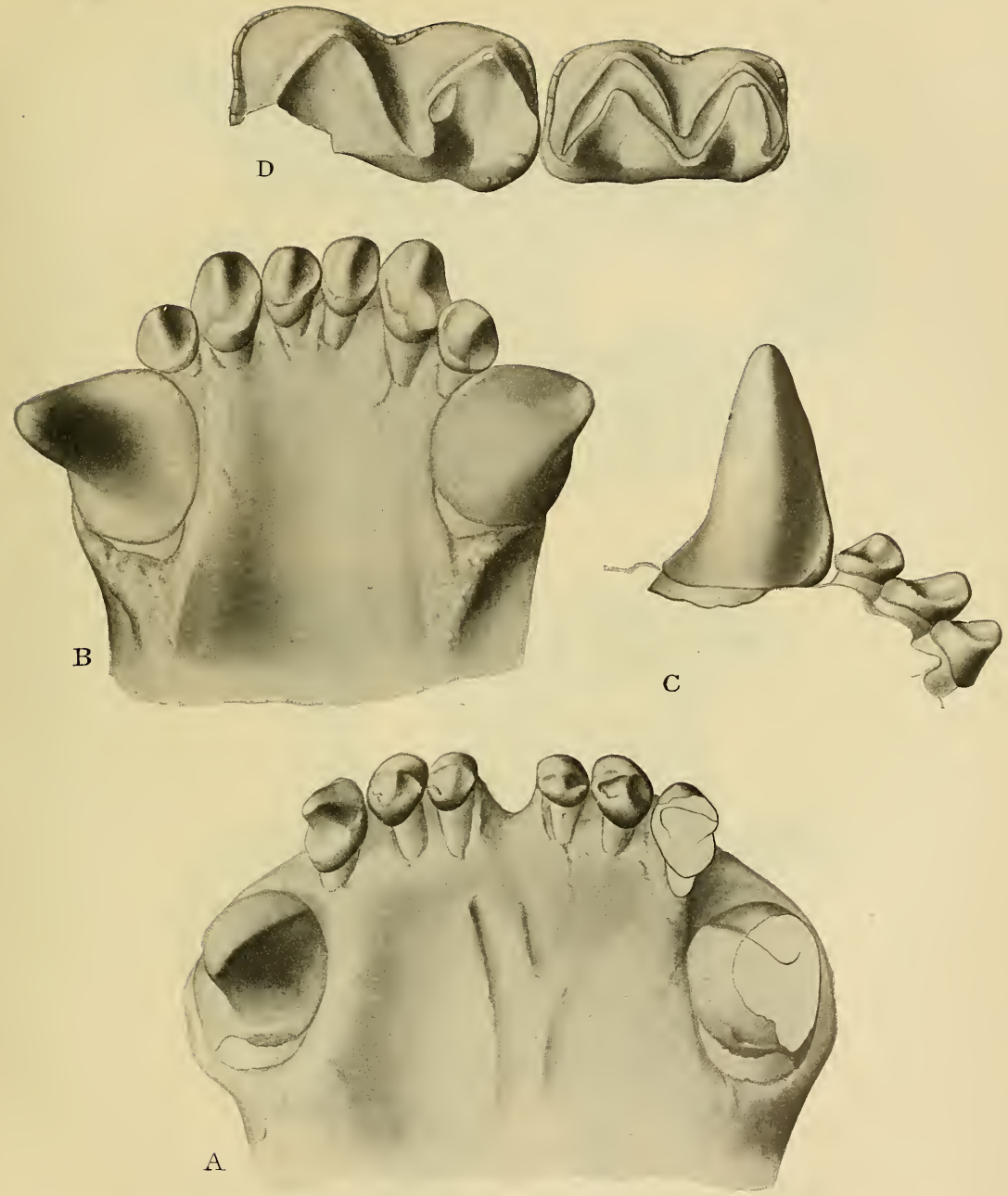
SKULL AND JAW REFERRED TO STHENODECTES INCISIVUS

A, Referred skull (Field Mus. 12168) and lower jaw (Field Mus. 12166), "*Amynodon* beds," level Uinta B 2, drawing reversed; one-fourth natural size; B, the same skull, basal view; C, the same jaw, top view



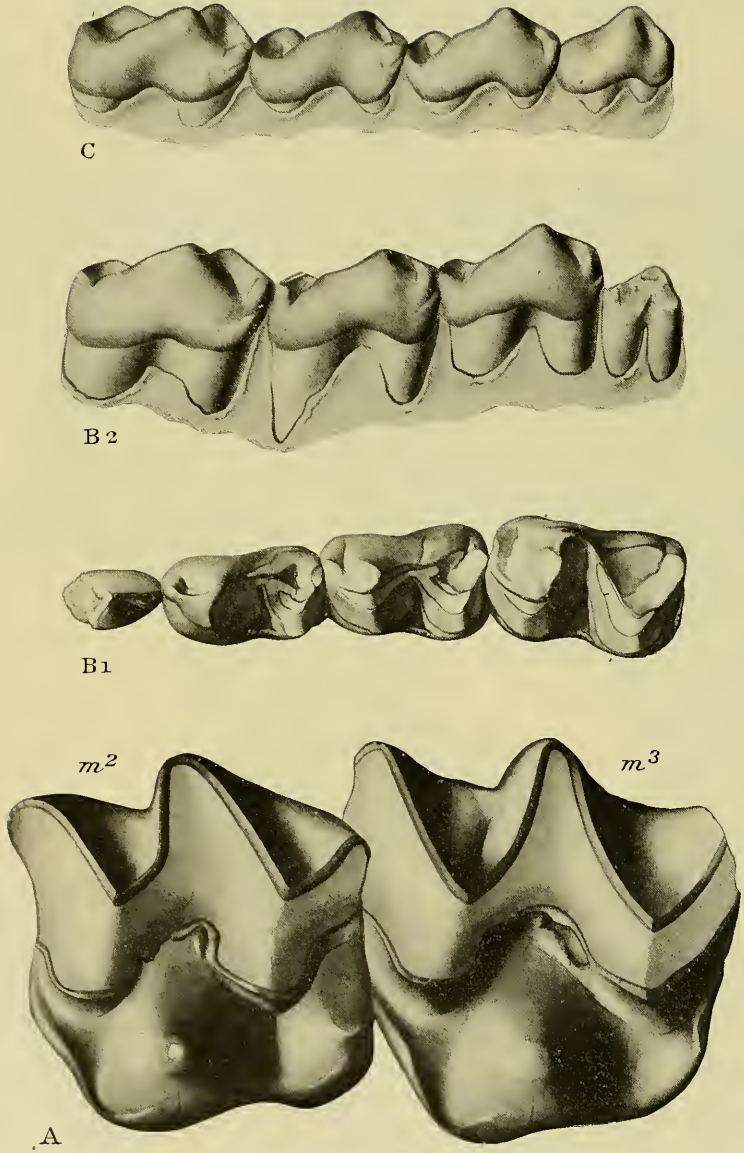
UPPER DENTITION OF MANTEOCERAS

Drawings by E. S. Christman. Natural size. (See pp. 367, 368, 371.) A, *Manteoceras manteoceras* (Am. Mus. 2353), lower beds, south of Haystack Mountain, Washakie Basin, Wyo., level Washakie A, premolar-molar series. B, M. *washakiensis*, type (Am. Mus. 13165), base of Haystack Mountain, Washakie Basin, Wyo., upper part of level Washakie A, upper jaw and dentition. C, M. *manteoceras* (Am. Mus. 1587), Henrys Fork, Bridger Basin, Wyo., upper premolars, external view



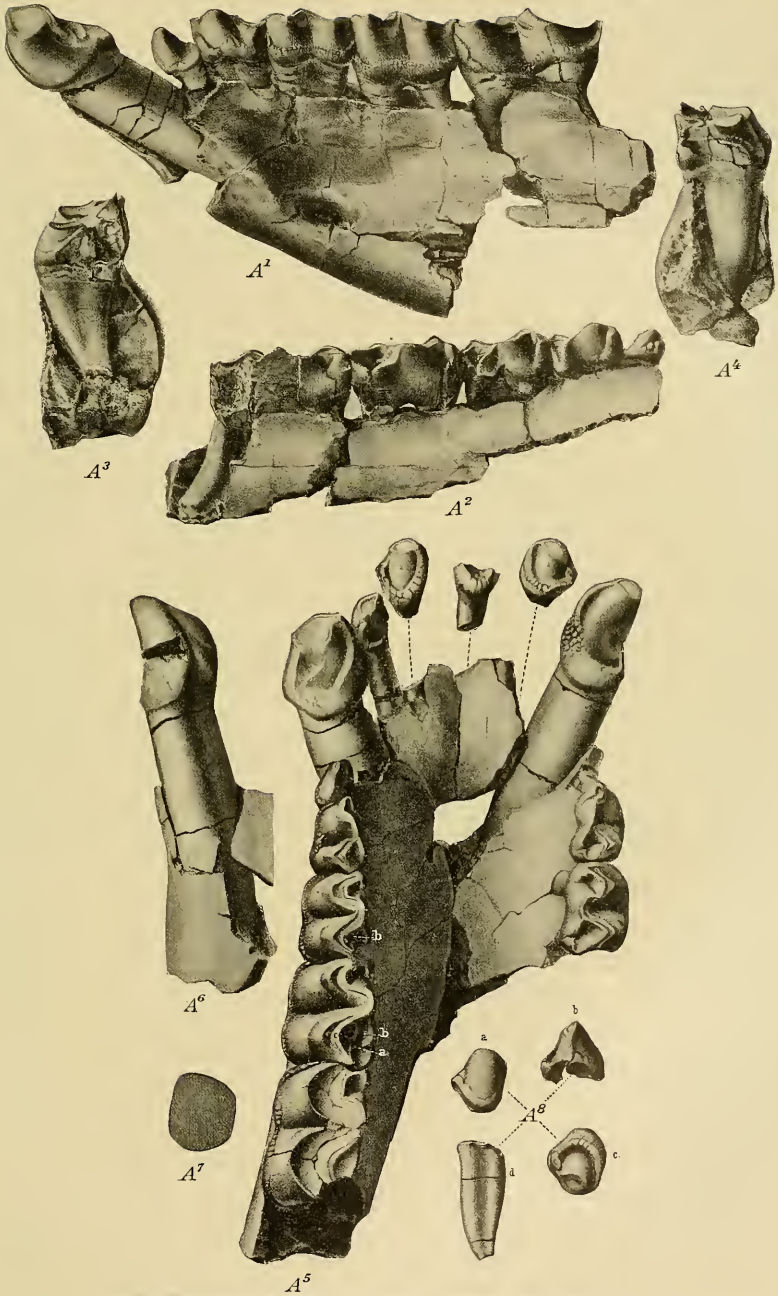
INCISORS AND CANINES OF PROTITANOTHERIUM EMARGINATUM

Drawings by E. S. Christman. Natural size. (See p. 378.) A, Type (Princeton Mus. 11242), level Uinta C 1 (of true Uinta formation), front part of upper jaw with crown view of canines and incisors; B, the same, front part of lower jaw with crown view of incisors and canines; C, the same, inner view of lower incisors and canines; D, the same, crown view of m_1, m_2, drawing reversed



UPPER AND LOWER TEETH OF PROTITANOTHERIUM

Progressive stages. Natural size. (See pp. 379, 380.) A, *Protitanotherium superbum*, type (Am. Mus. 2501), White River, Uinta Basin, Utah, level Uinta C (true Uinta formation), upper molars (m^2, m^3) found associated with type lower jaw. B_1, *P. superbum* (Am. Mus. 2501), lower premolars of type; B_2, the same, inner side view. C, *P. emarginatum*, type (Princeton Mus. 11242), inner side view of lower premolars



LOWER DENTITION OF BRACHYDIASTEMATHERIUM TRANSILVANICUM

(After Böckh and Maty; see p. 382.) One-half natural size. A, Type jaw, Andrásháza, Transylvania, Hungary, ?upper Eocene; A^1, outer side view of front part of lower jaw with canine and p_1–m_1; A^2, inner view of p_1–m_1; A^3, back view of m_1; A^4, front view of m_1; A^5, superior view of fragmentary lower jaw and dentition; A^6, external view of left lower canine; A^7, section of left lower canine; A^8, fragments of lower incisors

PLATE LXXI

PLATE LXXI

Lower Dentition of Mesatirhinus, Metarhinus, and Dolichorhinus

Drawings by E. S. Christman. Natural size. (See pp. 393, 394, 404, 424, 425)

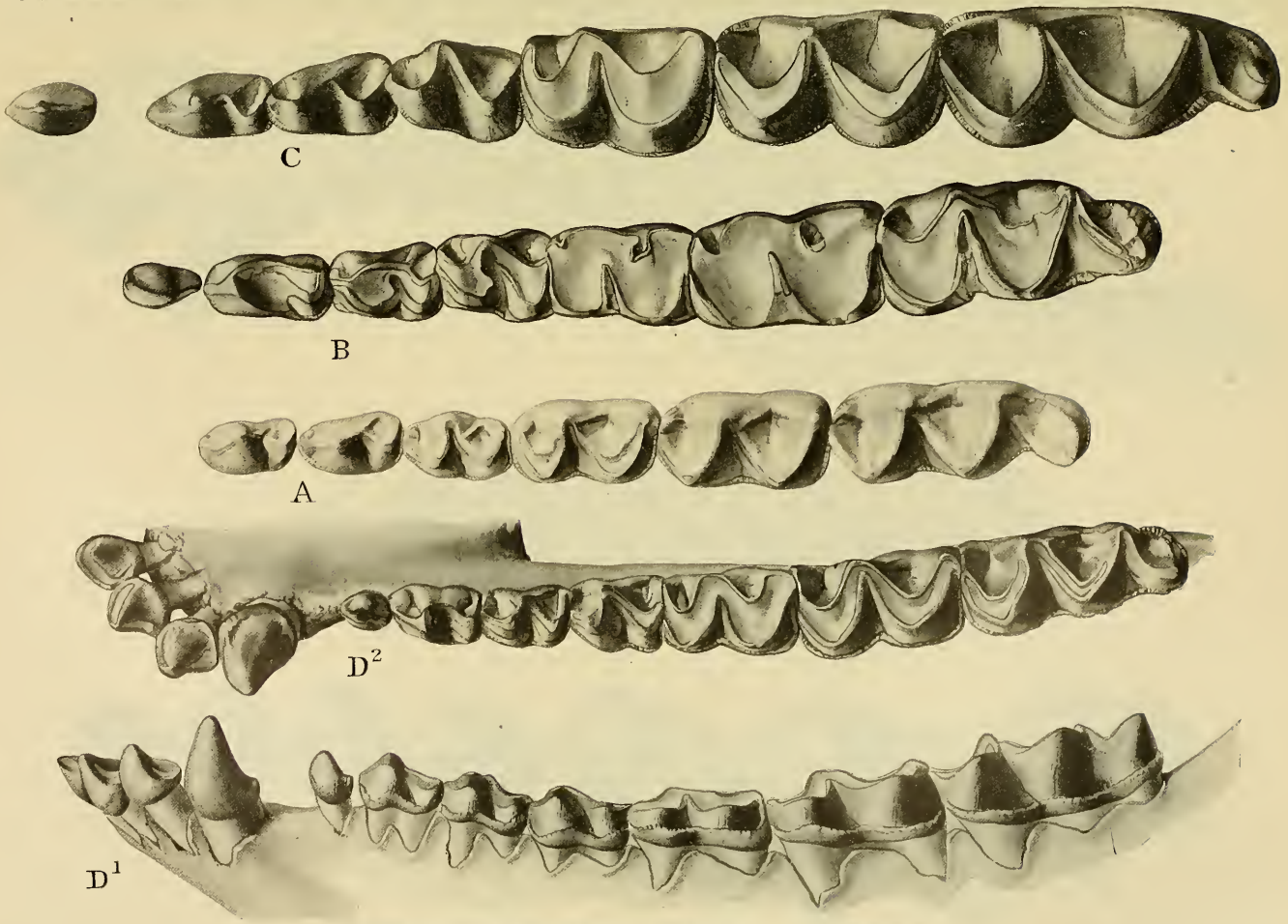
A, *Mesatirhinus petersoni* (Am. Mus. 1512), Laclede Meadows, Washakie Basin, Wyo., level?, left lower premolar-molar series, crown view.

B, *Mesatirhinus* sp. (Am. Mus. 2355), lower beds, south of Haystack Mountain, Washakie Basin, Wyo., level Washakie A(?) (Glove Spring), right lower premolar-molar series, crown view, drawing reversed.

C, *Dolichorhinus hyognathus* (Am. Mus. 1850), White River, Utah, level Uinta B 2, left lower cheek teeth (p_1–m_3), crown view.

D^1, *Metarhinus fluviatilis* (Am. Mus. 2059), White River, Utah, level Uinta B 1, external view of lower dentition.

D^2, The same, crown view.



LOWER DENTITION OF MESATIRHINUS, METARHINUS, AND DOLICHORHINUS

UPPER DENTITION OF MESATIRHINUS AND DOLICHORHINUS

Drawings by E. S. Christman. Natural size. (See pp. 393, 403, 413.) A, *Mesatirhinus megarhinus* (Am. Mus. 1514), Laclede Meadows, Washakie Basin, Wyo., level Washakie A. B, *M. petersoni* (British Mus., formerly Am. Mus. 1556), Big Bone Mountain, Henrys Fork, Bridger Basin, Wyo., level Bridger D (Sage Creek Mountain), upper cheek teeth, drawing reversed. C, *Dolichorhinus hyognathus* (Am. Mus. 1850), White River, Utah, level Uinta B 2, left upper cheek teeth, crown view; m^3, not yet fully in place, is seen obliquely

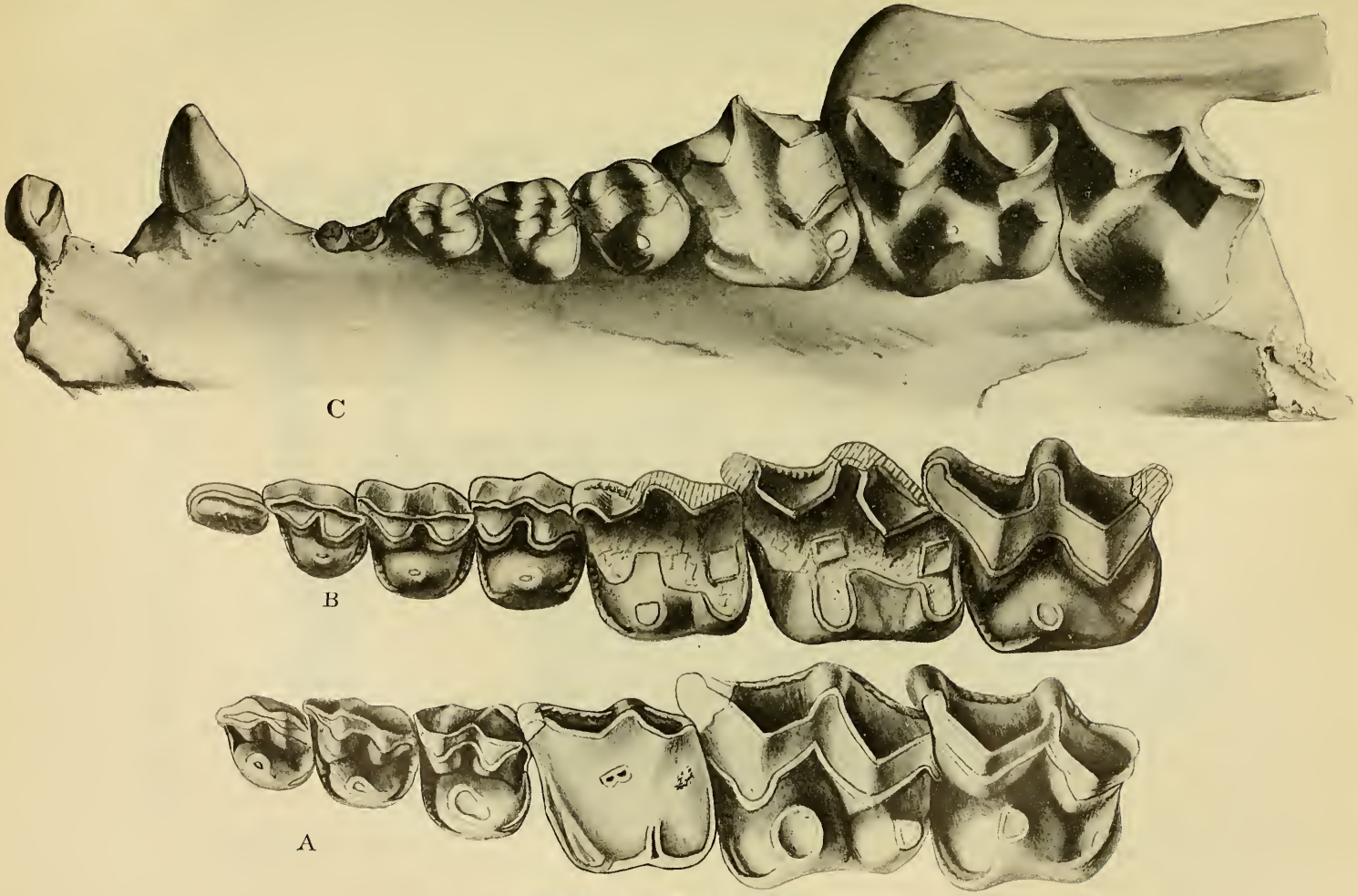
PLATE LXXIII

PLATE LXXIII

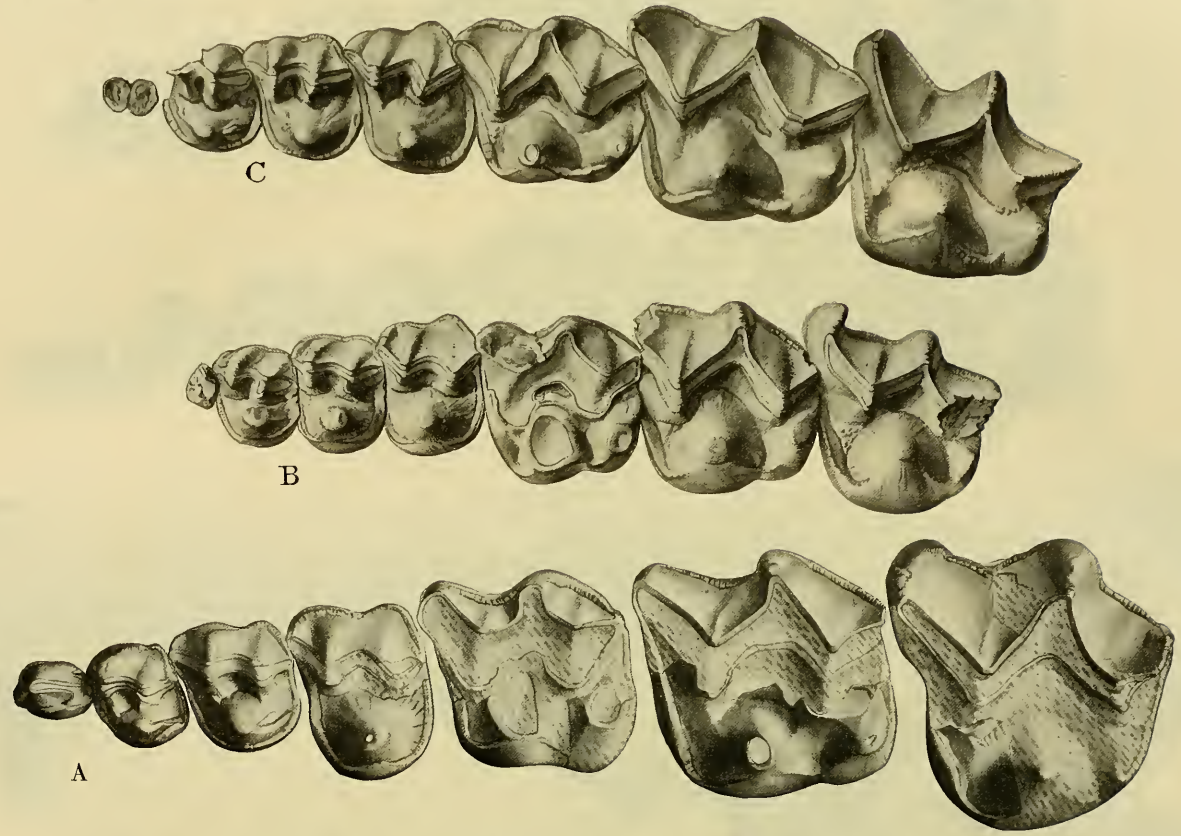
Upper Dentition of Dolichorhinus

Drawings A, B by Sidney Prentiss; C by E. S. Christman. Natural size. (See pp. 405, 406, 416)

A, *Dolichorhinus heterodon*, type (Carnegie Mus. 2340), level Uinta B 2 or C 1, upper cheek teeth (after Douglass), drawing reversed.
B, *D. longiceps*, type (Carnegie Mus. 2347), level Uinta B 1, right upper cheek teeth (after Douglass).
C, *D. intermedius*, type (Am. Mus. 1837), White River, Utah, level Uinta B 2, drawing reversed.



UPPER DENTITION OF DOLICHORHINUS

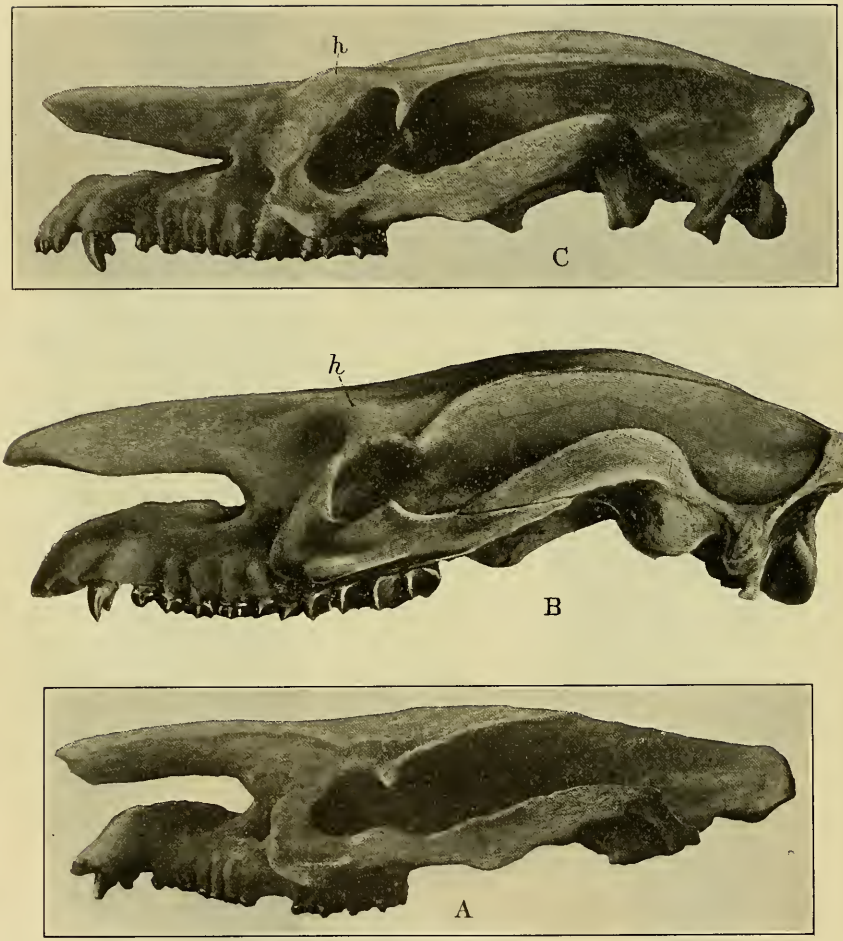


UPPER DENTITION OF DOLICHORHINUS, METARHINUS, AND RHADINORHINUS

Drawings by E. S. Christman. Natural size. (See pp. 403, 424, 433.) A, *Dolichorhinus vallidens*, paratype (Am. Mus. 5097), Mammoth Buttes, Bitter Creek, Washaki Basin, Wyo., level Washakie B, drawing reversed. B, *Metarhinus fluviatilis* (Am. Mus. 1946), White River, Utah, level Uinta B 2. C, *Rhadinorhinus diploconus* type (Am. Mus. 1863), White River, Utah, level Uinta B 2, drawing reversed

SKULLS AND JAW OF DOLICHORHINUS

(After E. S. Riggs; see pp. 405, 406, 417.) One-fourth natural size. A, *Dolichorhinus superior*, type (Field Mus. 12188), Uinta B 1. B, *D. fluminalis*, type (Field Mus. 12205), "*Amynodon* sandstone, Uinta B" (level Uinta B 2 of this monograph). C, *D. longiceps* (Field Mus. 12200), referred jaw



SKULLS OF DOLICHORHINUS, SIDE VIEW

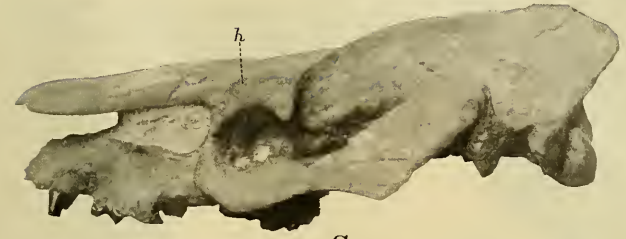
(After E. S. Riggs; see pp. 405, 406, 417.) One-fourth natural size. A, *Dolichorhinus superior*, type (Field Mus. 12188). B, *D. longiceps*, referred specimen (Field Mus. 12175), drawing reversed. C, *D. fluminalis*, type (Field Mus. 12205) "*Amynodon* sandstone," level Uinta B 2, drawing reversed

SKULLS OF DOLICHORHINUS, PALATAL VIEW

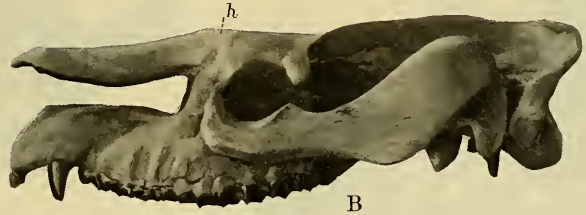
One-fourth natural size. A, *Dolichorhinus superior*, type (Field Mus. 12188; after E. S. Riggs). B, *D. fluminalis*, type (Field Mus. 12205), "*Amynodon* sandstone, Uinta B" (level Uinta B 2 of this monograph) (after E. S. Riggs). C, *D. longiceps*, type (Carnegie Mus. 2347), low in level Uinta B, palatal view (after Douglass)

SKULLS AND JAWS OF METARHINUS

After E. S. Riggs; see p. 421.) One-fourth natural size. A, *Metarhinus cristatus*, type (Field Mus. 12194), "Upper *Metarhinus* beds, White River Canyon." B, *M. earlei*, referred (Field Mus. 12187), "Upper *Metarhinus* beds," level Uinta B 1. C, *M. riparius*, type (Field Mus. 12186). D, *M. earlei*, referred lower jaw (Field Mus. 12178), "Upper *Metarhinus* beds," Uinta Basin, level Uinta B 1. E¹, *M. riparius*, referred lower jaw (Field Mus. 12195), "Upper *Metarhinus* beds," Uinta Basin, level Uinta B 1, side view, drawing reversed; E², the same, top view



C

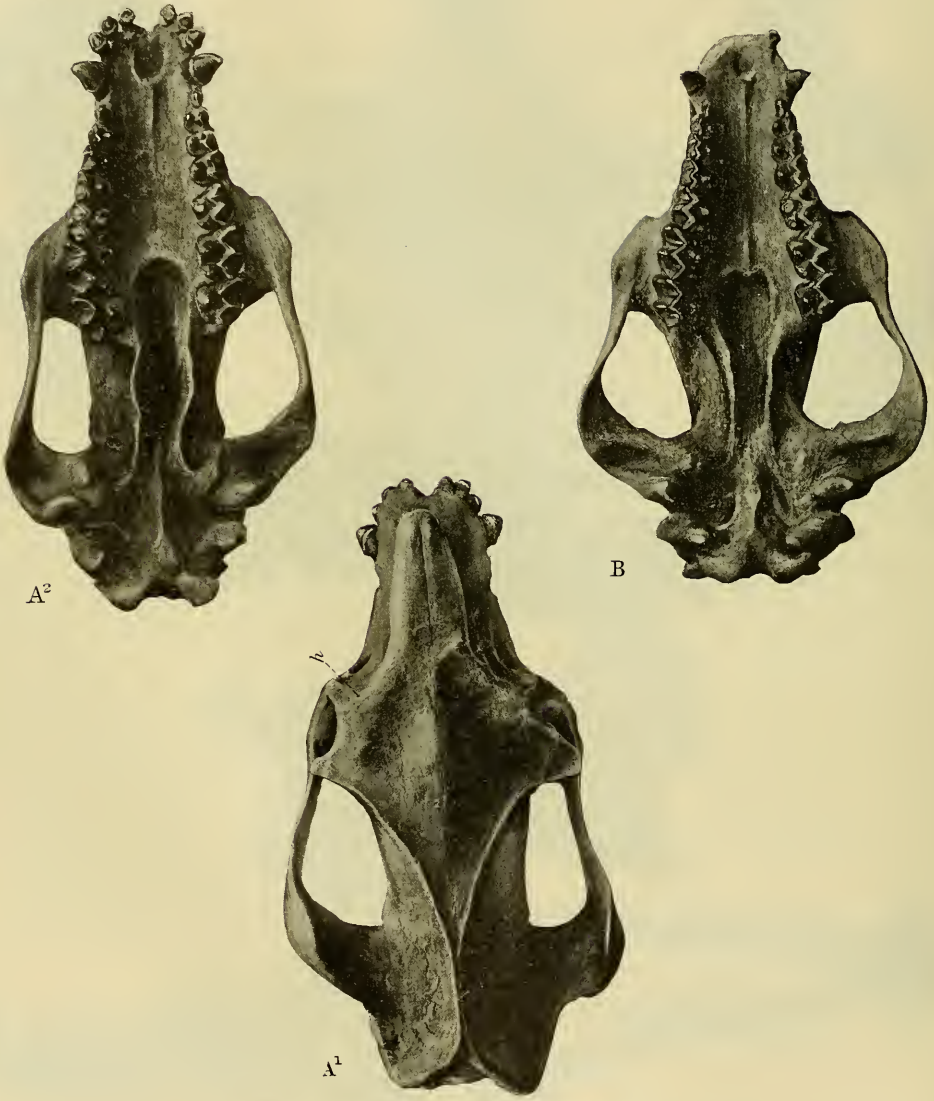


B

A

SKULLS OF METARHINUS

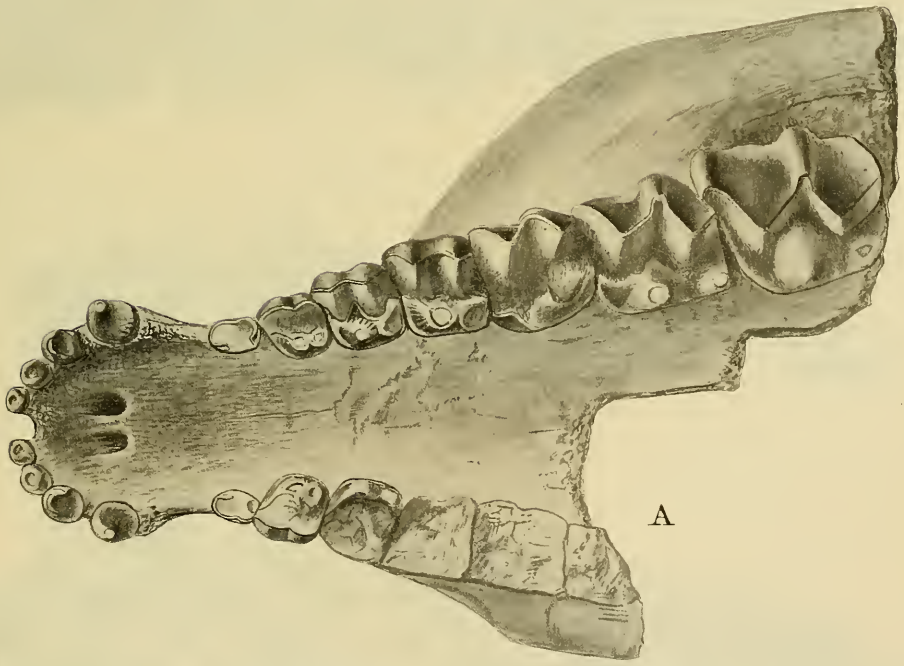
(After E. S. Riggs; see p. 421.) One-fourth natural size. A, *Metarhinus cristatus*, type (Field Mus. 12194), drawing reversed. B, *M. earlei*, referred (Field Mus. 12187), "Upper *Metarhinus* beds" (level Uinta B 1), Uinta Basin, drawing reversed. C, *M. riparius*, type (Field Mus. 12186), "Upper *Metarhinus* beds" (level Uinta B 1), Uinta Basin, drawing reversed



SKULLS OF RHADINORHINUS AND METARHINUS

(After E. S. Riggs; see pp. 426, 430.) One-fourth natural size. A^1, *Rhadinorhinus abbotti*, type (Field Mus. 12179), "Upper *Metarhinus* beds" (level Uinta upper B 1), Uinta Basin, top view; A^2, the same, basal view. B, *M. earlei*, referred (Field Mus. 12187), "Upper *Metarhinus* beds," Uinta Basin, basal view

B



A

UPPER DENTITION OF EOTITANOTHERIUM OSBORNI AND DIPLACODON ELATUS

(After Peterson; see p. 435.) Drawings by Sidney Prentiss. One-half natural size. A, *Eotitanotherium osborni*, type (Carnegie Mus. 2859), upper jaw and dentition. B, *Diplacodon elatus*, type (Yale Mus. 11180), upper dentition

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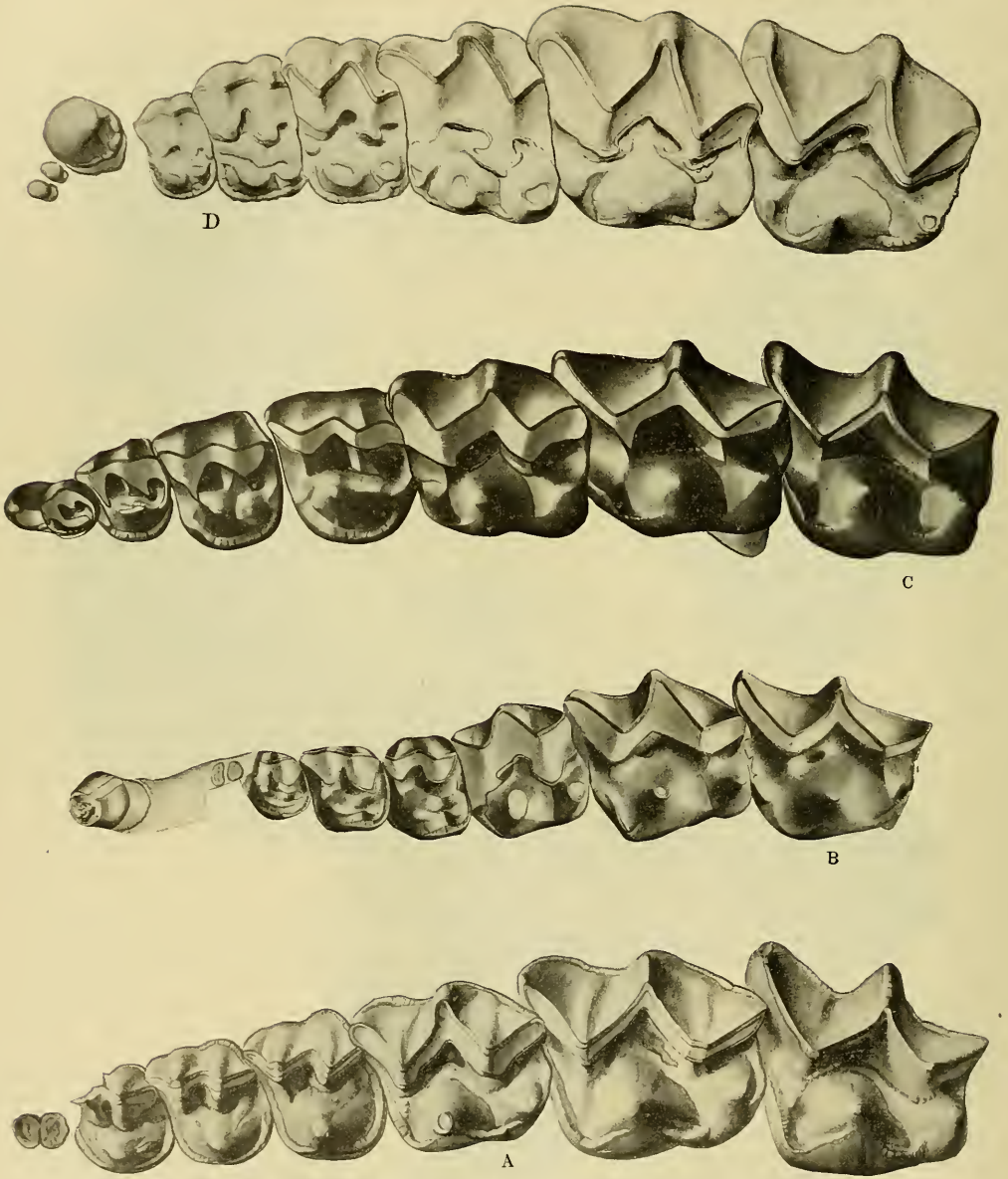


COMPARISON OF UPPER TEETH OF RHADINORHINUS, DIPLACODON, MENODUS, AND BRONTOTHERIUM

Drawings by E. S. Christman. A is natural size; in B, C, and D the premolar-molar series is reduced to the same length as in A. (See pp. 434, 474.) A, *Rhadinorhinus diploconus*, type (Am. Mus. 1863), White River, Utah, level Uinta B 1 or 2. B, *Diplacodon elatus*, type (Yale Mus. 10320), level Uinta C(?). C, *Menodus* cf. *M. proutii* (Carnegie Mus. 558), Chadron formation. D, *Brontotherium gigas elatus* (Am. Mus. 492), Cheyenne River, S. Dak., Chadron formation

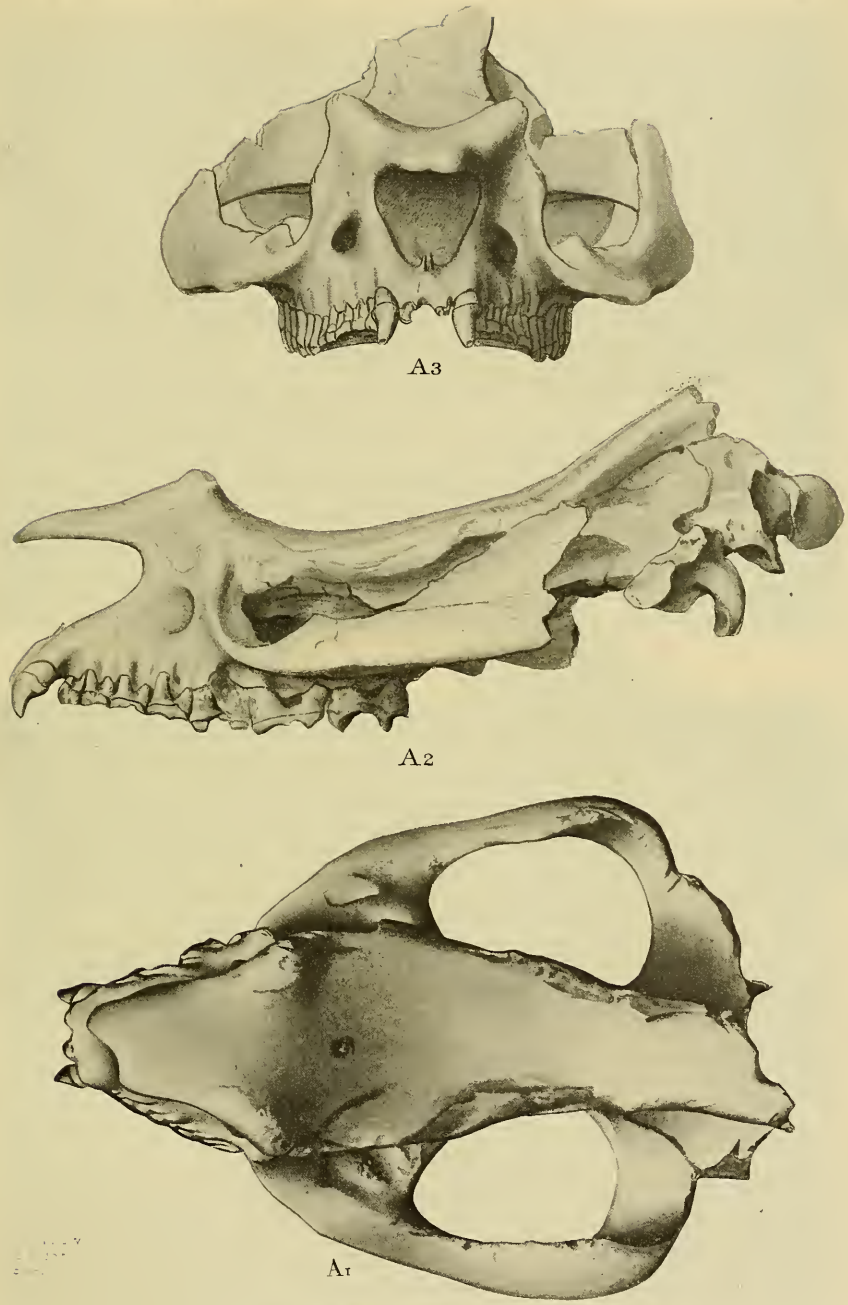
PLATE LXXXIII

PLATE LXXXIII

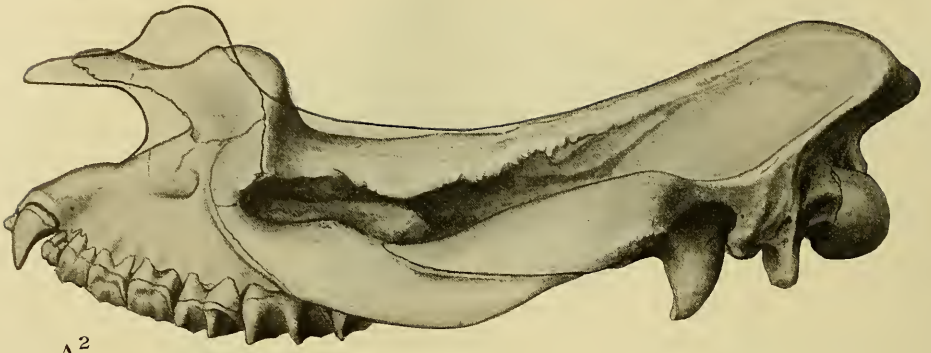
Skull of Brontops brachycephalus

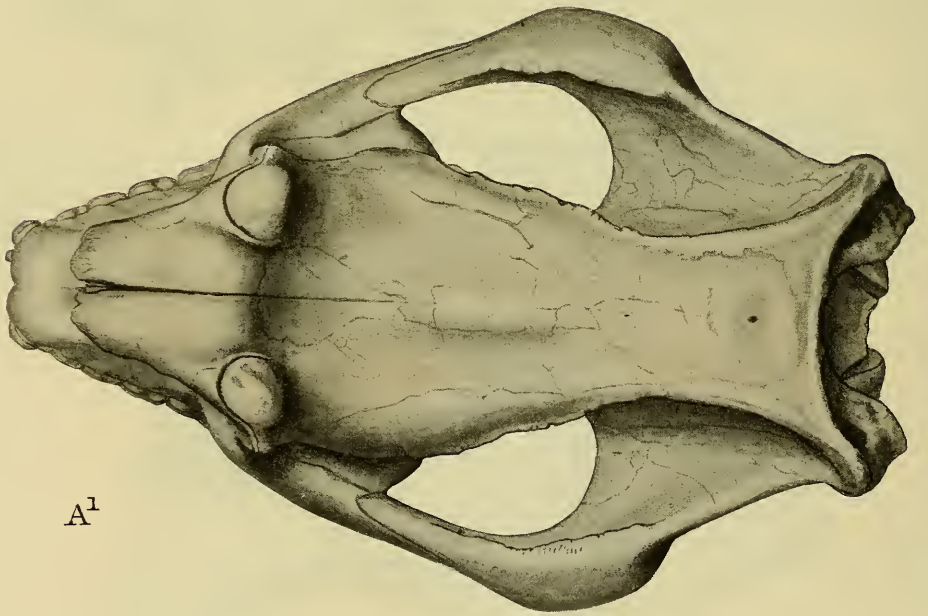
Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 484 and Pl. LXXXVII)

Nat. Mus. 4947, skull B, paratype, female; Big Badlands, S. Dak., "west side of Quinn Draw, near the Cheyenne River" (J. B. Hatcher); *Titanotherium* zone (= Chadron formation) of South Dakota, level lower A (Hatcher). A_1, Top view; A_2, side view; A_3, front view. The female sex is inferred from the small horns, slender zygomata, less brachycephalic proportions, and weak canines. The horns are smaller and more primitive than in any other known Oligocene titanothere; the skull comes from an extremely low level in the "*Titanotherium* beds" (14.4 feet above the Pierre shale and 130.6 feet below the top of the "*Titanotherium* beds," according to Hatcher) and seems to represent a slightly more primitive stage than the type of the species.



SKULL OF BRONTOPS BRACHYCEPHALUS

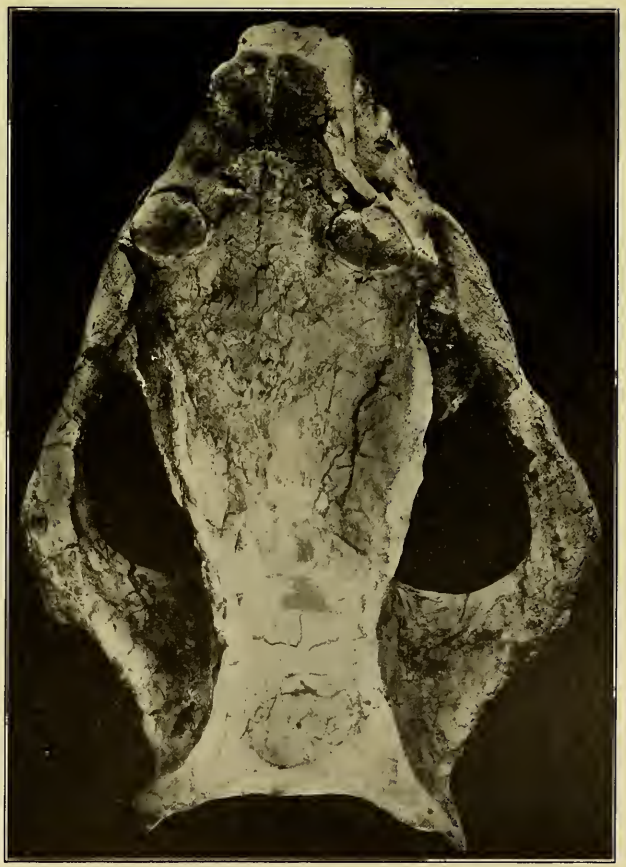




SKULL OF BRONTOPS BRACHYCEPHALUS

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 487, also Pls. LXXXV and LXXXVI.) Nat. Mus. 4258, skull F, female, referred to B. *brachycephalus*. (According to the records in the U. S. National Museum this is skull F of the 1886 collection, not skull F of Hatcher's diary of 1887.) Big Badlands, S. Dak., Chadron formation (*Titanotherium* zone), level middle B (Hatcher). This immature skull is vertically crushed, so that the nasals and horns are tilted upward and backward, and the apparent breadth of the skull is increased. The sutures show the participation of both nasals and frontals in the horns. The lacrimal is represented as entering the outer ridge of the horn. The skull is larger than that of the type and comes from a higher level. The dental measurements are much smaller than in any skull referred to B. *dispar*

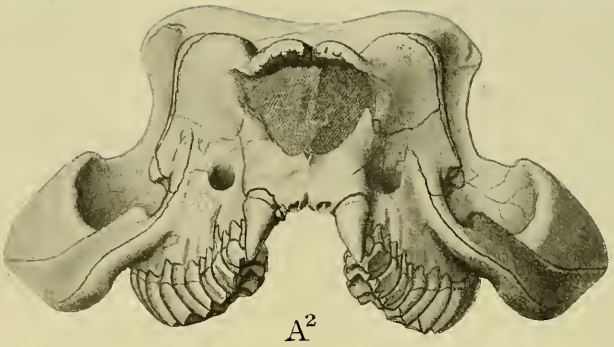
A

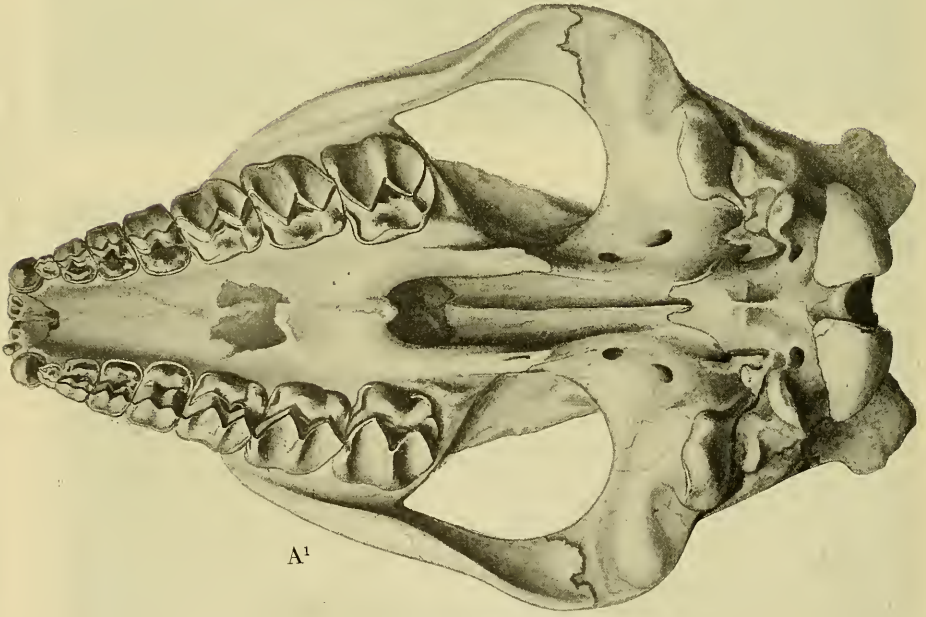


B

SKULLS OF BRONTOPS BRACHYCEPHALUS

One-fourth natural size. (See p. 488.) A, Nat. Mus. 4259, skull M, male, referred, Big Badlands, S. Dak., Chadron formation (*Titanotherium* zone), level lower B (Hatcher). This skull is recorded from a higher level (55.6 feet above Pierre shale) than that of the type and is much more progressive in its longer horns and more pronounced brachycephaly. It is not sufficiently advanced, however, to be placed in B. *dispar*, from which it differs in the smaller dimensions, especially of the dentition. B, Nat. Mus. 4258, skull F, referred. (See Pl. LXXXIV)





SKULL OF BRONTOPS BRACHYCEPHALUS

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 488, also Pls. LXXXIV and LXXXVIII.) Nat. Mus. 4258, skull F, referred, Big Badlands, S. Dak., Chadron formation (*Titanotherium* zone), level middle B (Hatcher). A¹, Basal view, a partial reconstruction, the actual condition being shown in Plate LXXXVIII. The tooth rows as here represented are somewhat too rectilinear, and the details of the premolars are incorrect in several points. The suture between the basi-, pre-, and alisphenoids is well shown. A², Front view showing the sutural relations of the frontals, nasals, lacrimals, maxillaries, malars, etc., relations which are essentially the same as in Eocene titanotheres.

PLATE LXXXVII

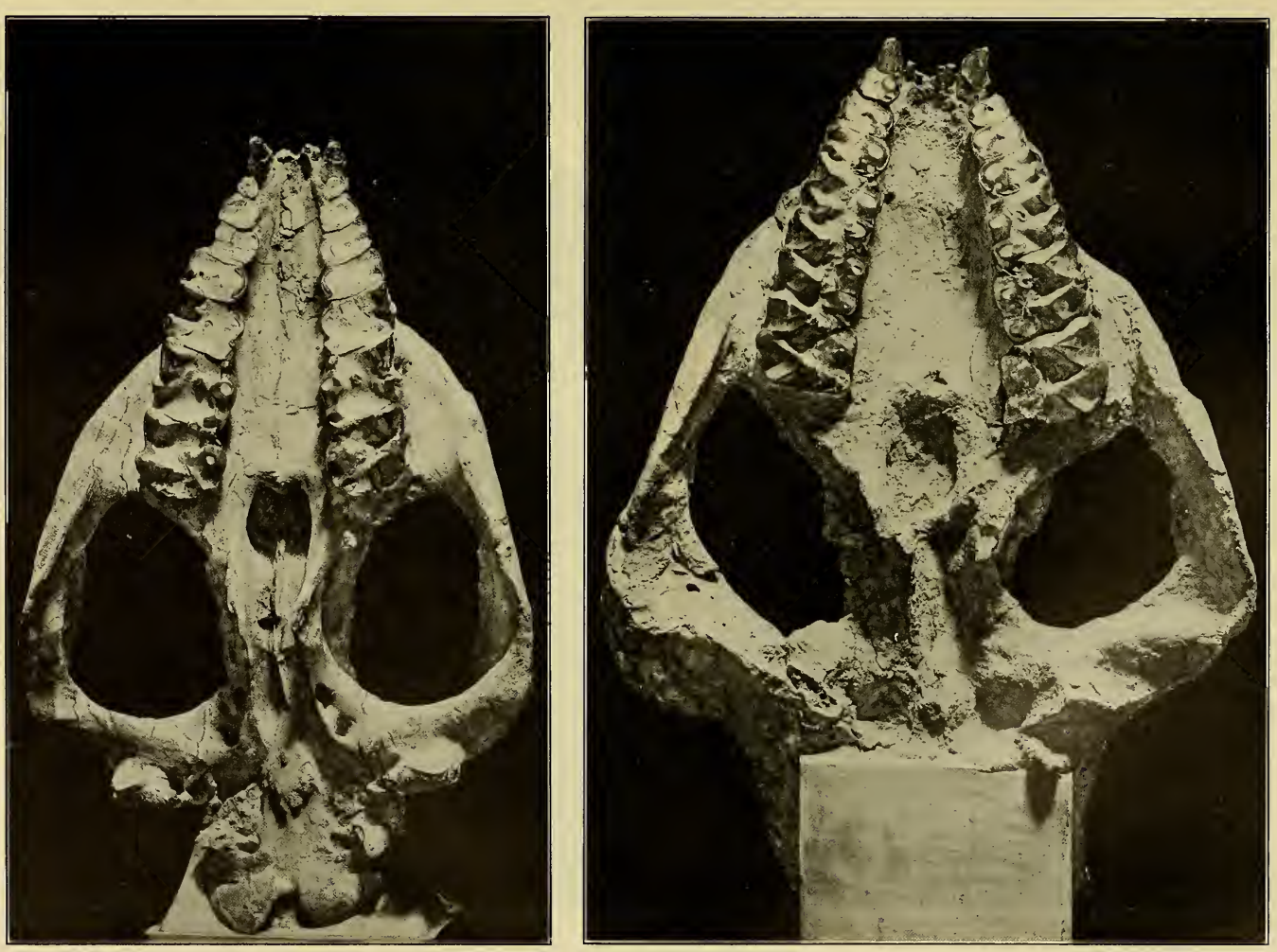
PLATE LXXXVII

Skulls of Brontops brachycephalus

One-fourth natural size. (See pp. 484, 485, also Pl. LXXXIII)

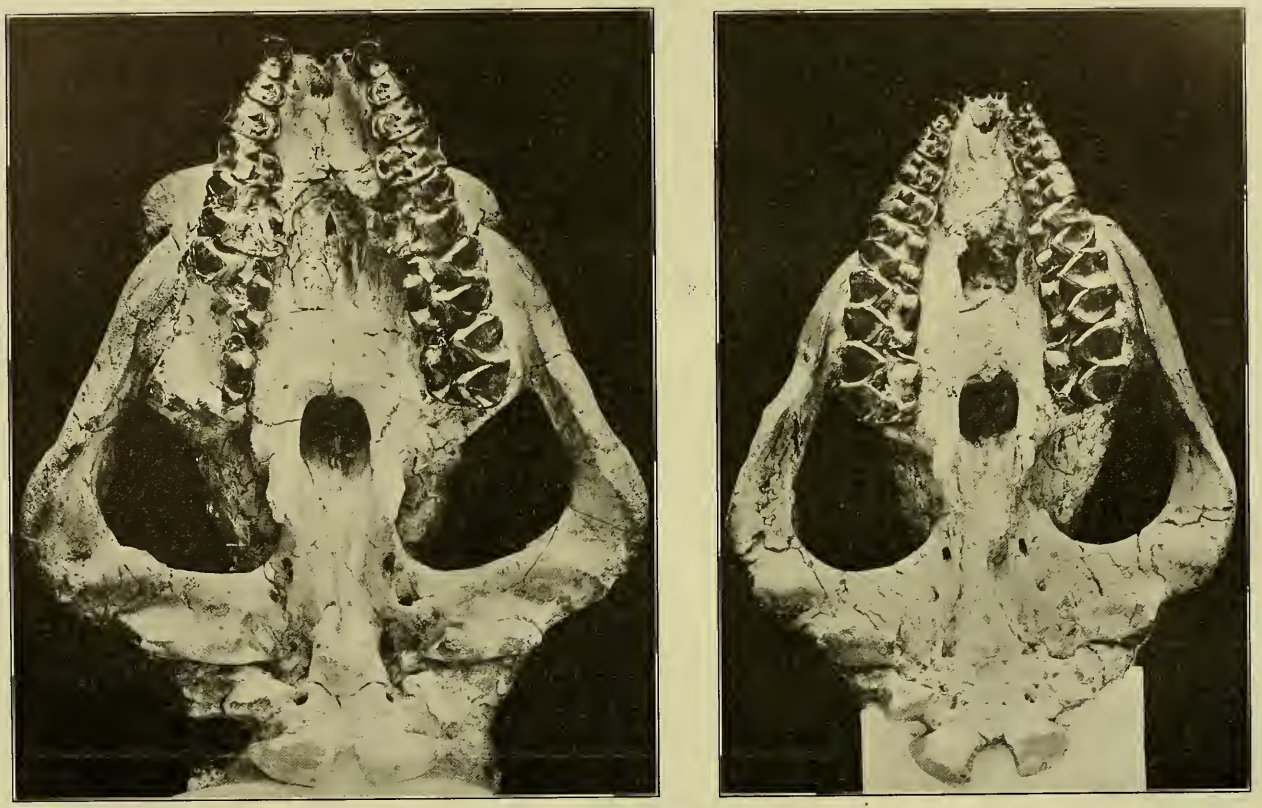
A, Paratype (Nat. Mus. 4947), skull B, female, Big Badlands, S. Dak., "west side of Quinn Draw, near the Cheyenne River" (J. B. Hatcher); *Titanotherium* zone (=Chadron formation), lowest levels (14.4 feet above Pierre shale). As compared with the type male skull (B) this aged female is smaller, more elongate, and slenderer, with small canines and unexpanded zygomata. The much worn molar teeth appear somewhat more primitive than those of the type, especially m^3.

B, Type (Nat. Mus. 4261), skull c, male, Big Badlands (probably Corral Draw), S. Dak., near base of lower *Titanotherium* zone. Generic affinity with *Brontops robustus* is indicated by the presence of one or two round-topped incisors on each side (the inner pair often drop out in adults), the stout canines, the retarded postero-internal cusps on p^4, the general brachycephalic form of the skull, and the character of the horns.



A B

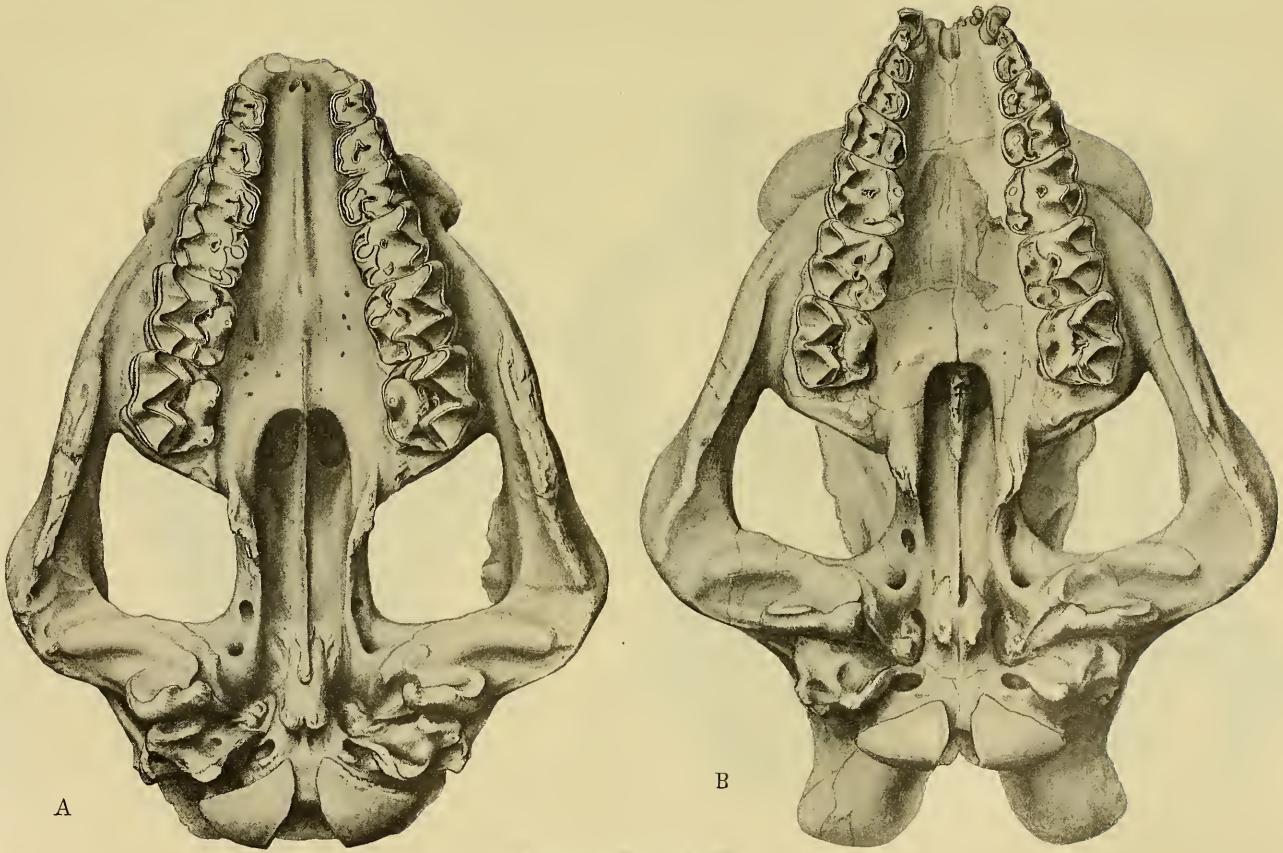
SKULLS OF BRONTOPS BRACHYCEPHALUS



A B

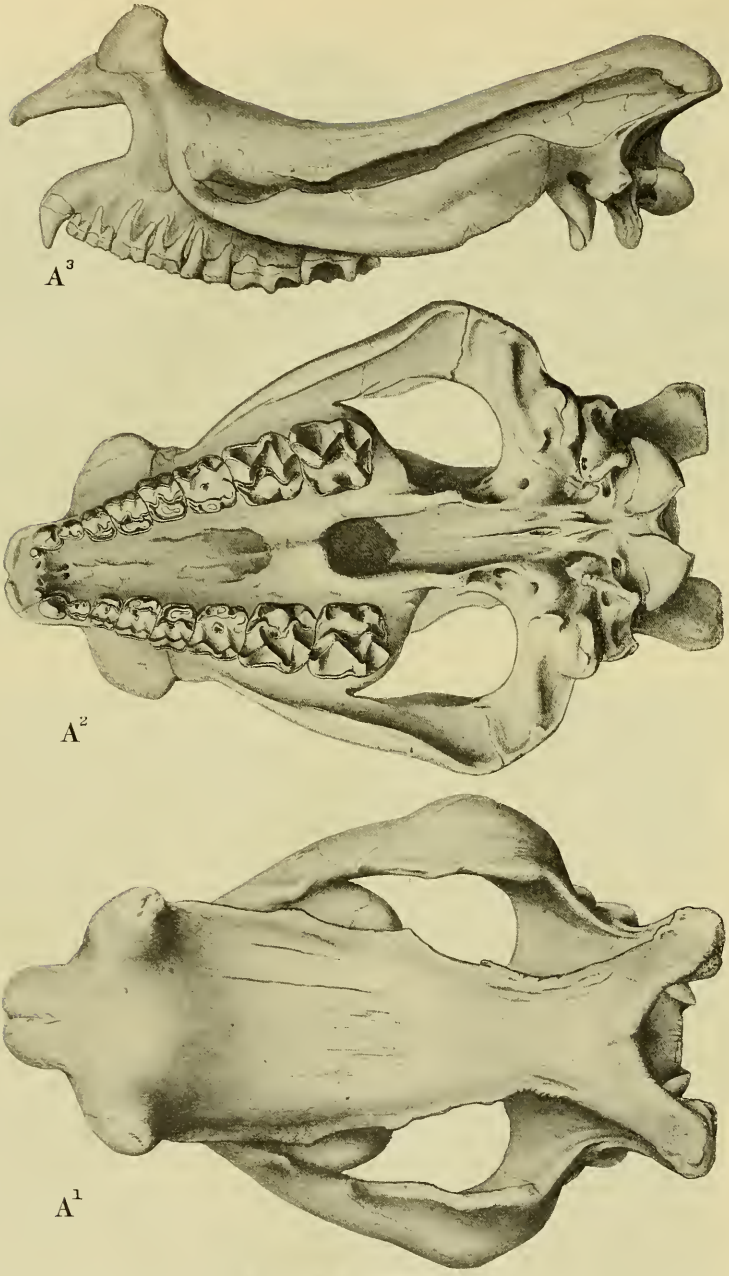
SKULLS OF BRONTOPS BRACHYCEPHALUS AND B. DISPAR

One-fourth natural size. (See pp. 488, 489, also Pls. LXXXVI and XCI.) A, *Brontops dispar* (Nat. Mus. 4290), skull K, referred (one of the 1886 skulls, "62 feet above Ft. Pierre"—Hatcher), type of B. *validus* Marsh, Big Badlands, S. Dak., *Titanotherium* zone, middle level of middle beds (Hatcher). This species, typical of level middle B of the *Titanotherium* zone (Chadron formation), carries the *Brontops* line in the direction of *B. robustus*. The skull is brachycephalic, with large broad molars, premolars with rounded internal and well-defined external cingula. B, B. *brachycephalus* (Nat. Mus. 4258), skull F, referred, Big Badlands, S. Dak., *Titanotherium* zone, level middle B (Hatcher). Among the generic characters shown in these two skulls are, skull brachycephalic, basis cranii short, $\frac{12}{1}$, canines stout and of moderate length, premolars with internal and external cingula, postero-internal cusp of premolars retarded (especially on p^1), premolars and molars relatively broader than in *Menodus*



SKULLS OF BRONTOPS DISPAR

Plate prepared under the direction of Professor Marsh. One-fifth natural size. (See p. 489, also Pl. LXXXVIII.) A, Nat. Mus. 4248, skull G, locality uncertain, Chadron formation. A large and progressive *B. dispar* of advanced age. The grinding teeth are large and of advanced type. B, Nat. Mus. 4290, skull K, type of *B. validus* Marsh, Big Badlands, S. Dak., *Titanotherium* zone, middle level of middle beds (Hatcher). These skulls show the robustness and brachycephaly characteristic of this genus



SKULL OF BRONTOPS DISPAR

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See p. 489.) Nat. Mus. 4245 (erroneously lettered skull P, according to J. B. Hatcher), locality uncertain, Chadron formation. A^1, Top view; A^2, palatal view; A^3, side view. This skull exhibits a certain resemblance to *Allops marshi*, but the measurements are closer to those of *B. dispar*. The original is badly crushed and as here reconstructed the tooth rows may perhaps be too rectilinear

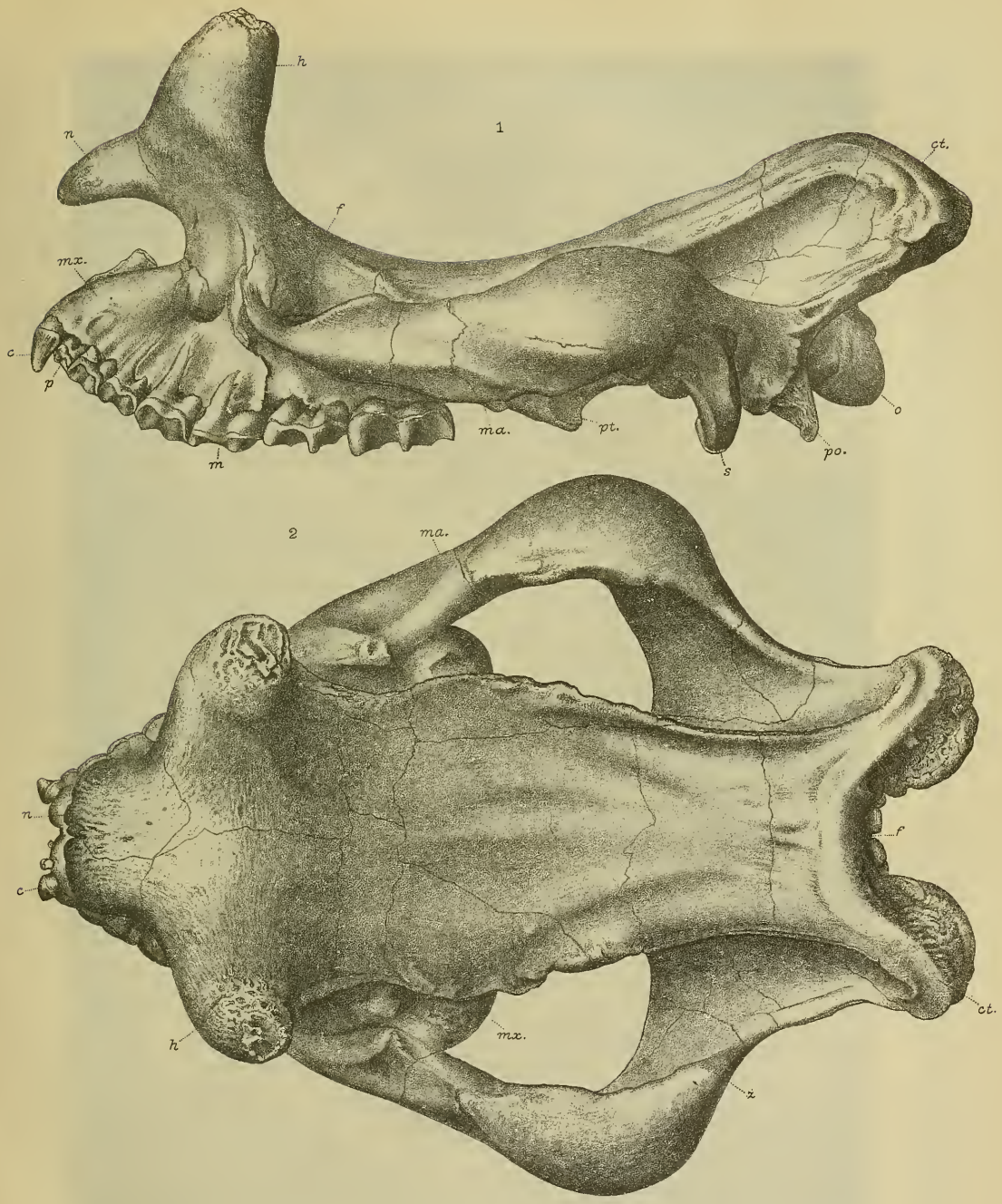
PLATE XCI

PLATE XCI

Skull of Brontops dispar

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See pp. 489, 490)

Nat. Mus. 4290, skull K, Big Badlands, S. Dak., *Titanotherium* zone, level middle B (J. B. Hatcher). Referred male skull, type of *B. validus*. Vertical crushing has lessened the vertical diameters of the skull top and tilted the horns upward and backward. The skull is very robust and brachycephalic. The stout horns are rounded in section, with a rugose area at the tip for the attachment of the thickened epidermal cap. The general conformation of the skull, especially of the nasals and horns, suggests possible ancestry to *B. robustus*.



SKULL OF BRONTOPS DISPAR

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A B

SKULLS OF BRONTOPS DISPAR

One-fifth natural size. (See pp. 489, 490, also Pl. XCI.) A, Nat. Mus. 4290, skull K, Big Badlands, S. Dak., *Titanotherium* zone, level middle B (J. B. Hatcher); an older and more robust skull with stouter nasals, horns, and zygomata. B, Nat. Mus. 4703, skull f, Big Badlands (probably Indian Draw), S. Dak., *Titanotherium* zone, level certainly middle B, 62 feet above Pierre shale (J. B. Hatcher); a younger, somewhat more slender skull

PLATE XCIII

PLATE XCIII

Skulls of Brontops dispar

About one-fifth natural size. (See pp. 490, 492)

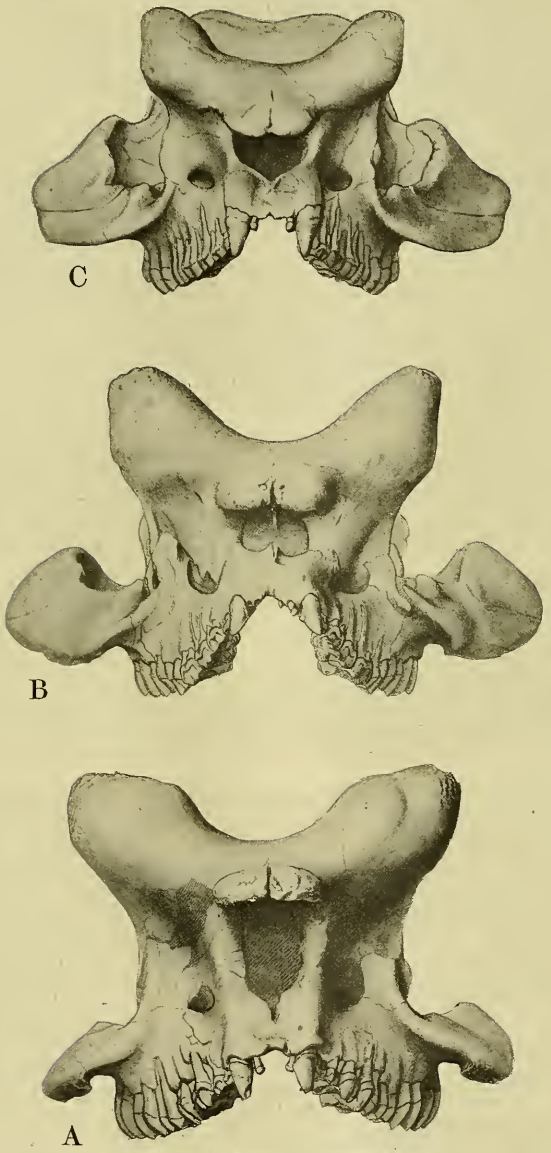
A, Nat. Mus. 1217, skull p (?*Allops serotinus*), Big Badlands (probably Indian Draw), S. Dak., *Titanotherium* zone, level "somewhat doubtful, probably lower C" (Hatcher). This very progressive skull shows certain of the characters common to *Brontops*, *Allops*, and *Menodus*, in contrast with the *Brontotherium-Megacerops* group.

B, Nat. Mus. 4941, skull D, type, Hat Creek, Nebr., *Titanotherium* zone, level middle B (Hatcher). This laterally crushed skull, the genotype of *Brontops*, was evidently brachycephalic, with stout rounded horns, thick nasals, short thick canines, and heavy zygomata. The horns are well in front of the orbits. It is thus more or less intermediate in form between the highly specialized *B. robustus* and the primitive *B. brachycephalus* and also exhibits convergent resemblance to the type of *Brontotherium tichoceras*.

A

B

SKULLS OF BRONTOPS DISPAR



SKULLS OF BRONTOPS DISPAR

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See pp. 489, 491, also Pls. XCI, XCII, and XCIII.) A, Nat. Mus. 4941, skull D, type, reconstructed from the crushed original; only the front parts of the zygomata are shown. B, Nat. Mus. 4290, skull K, type of B. *validus*. The skull is crushed downward, thus lessening the height of the narial opening. The horns are rounded in mid-section, with slender tips, the nasals stout and broad distally, the buccal swellings heavy. The inner incisors are small or absent. C, Nat. Mus. 4245 (erroneously lettered P). A more slender skull which somewhat resembles *Allops marshi*. (See Pl. CXIV)

SKULL OF BRONTOPS ROBUSTUS?

One-fourth natural size. (See p. 497.) Princeton Mus. 10061, Chadron formation. The specific reference is somewhat doubtful; the skull resembles that of the type of B. *robustus* in the forward pitch of the short horns, in the short nasals, and in the form of the incisors and canines

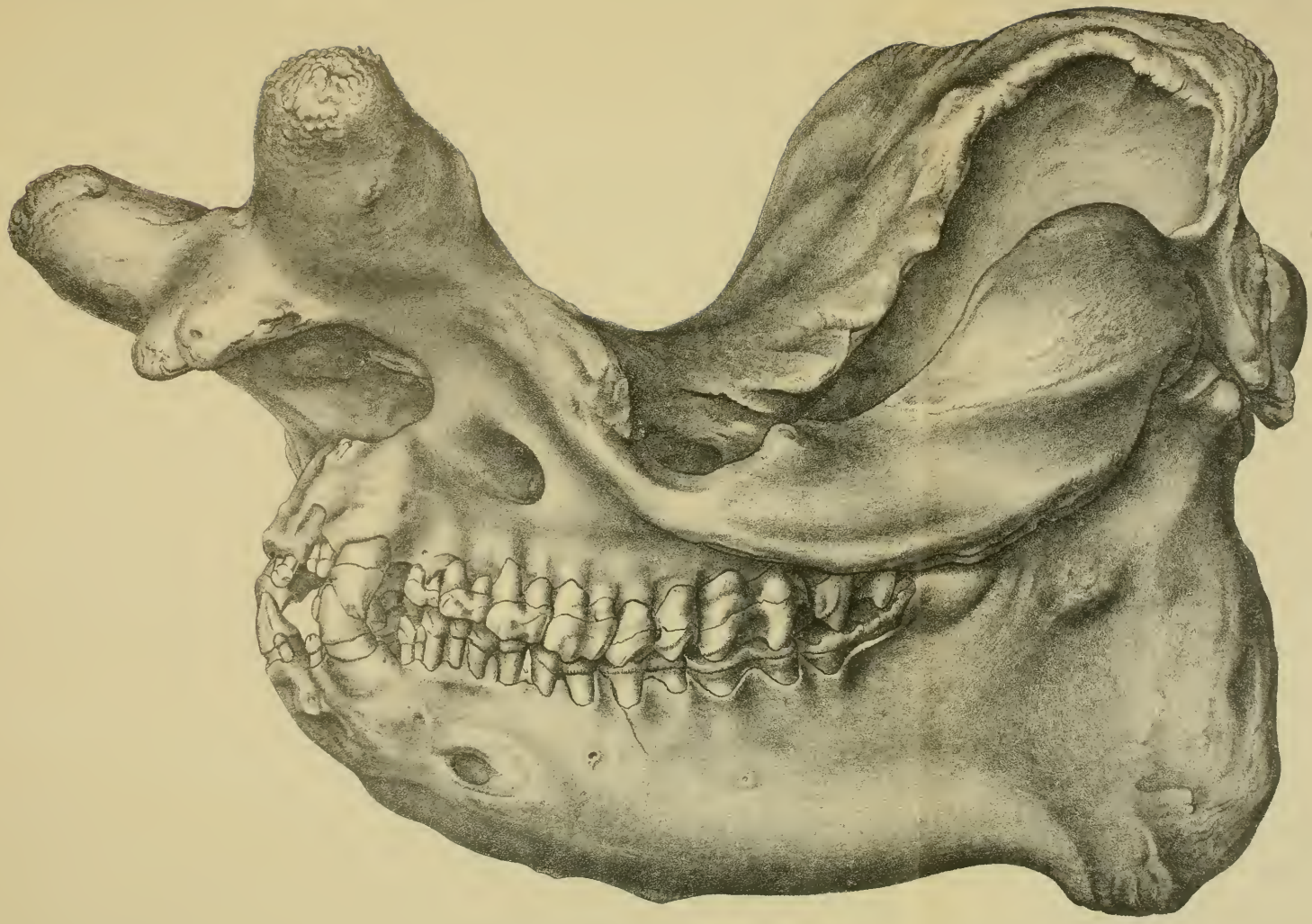
PLATE XCVI

PLATE XCVI

Type Skull and Jaw of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-third natural size. (See p. 494)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. This great skull represents the culminating member of the *Brontops* phylum. It is highly specialized in its massiveness and great breadth, in the position of the horns, which are far in front of the orbits, in the great development of the external basal ridge of the horns, in their flattened basal section, and in the thickness and abbreviation of the nasals. Relationship with *Brontops dispar* is indicated by the shortness of skull top and base, by the absence of the mid-parietal eminence, and by the form of the premolars. Convergent resemblances to *Brontotherium* are seen in the flatness of the horns, abbreviation of nasals, swollen zygomata, short, robust canines, and heavy round-topped incisors.



TYPE SKULL AND JAW OF BRONTOPS ROBUSTUS

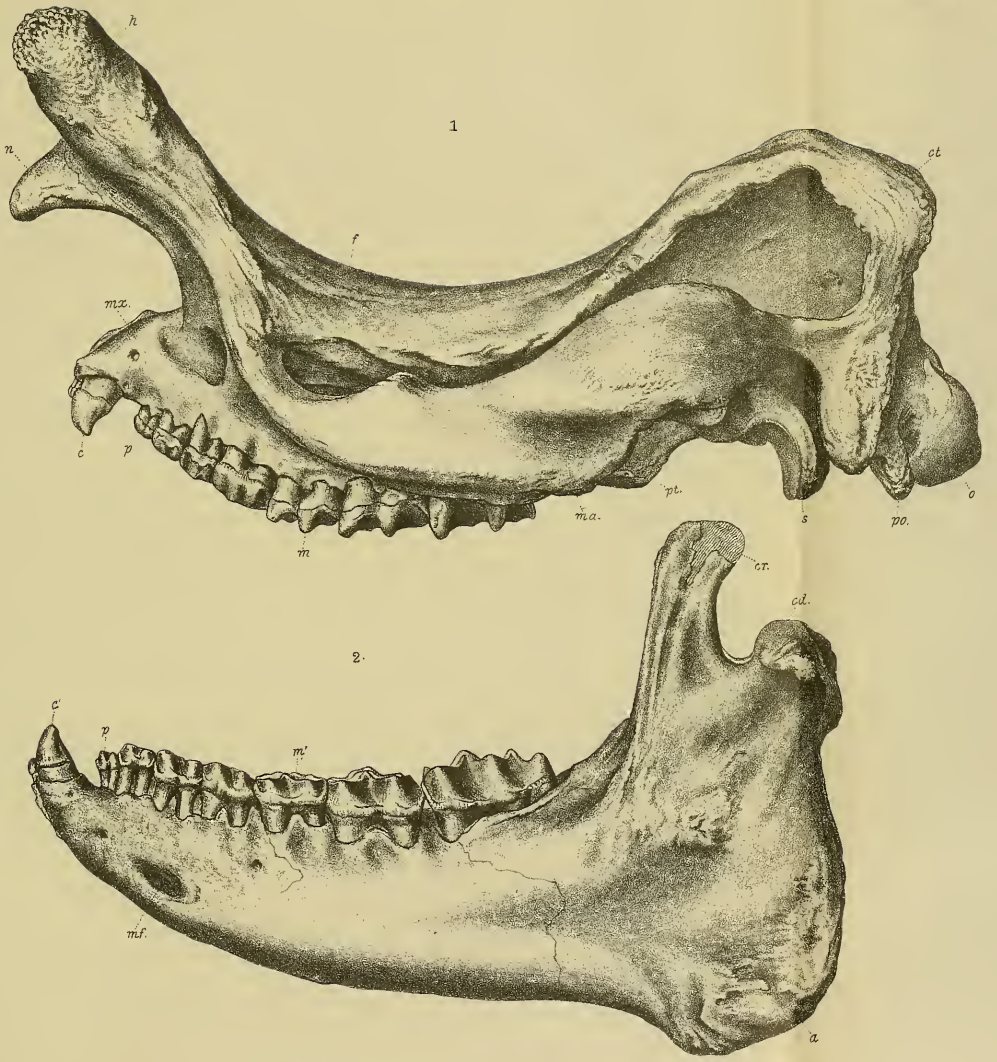
PLATE XCVII

PLATE XCVII

Type Skull and Jaw of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 494, also Pl. XCVI)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. Slight vertical crushing may have somewhat diminished the vertical diameters. The skull is relatively much shorter than in *Brontotherium*, and the occiput is not produced backward.



TYPE SKULL AND JAW OF BRONTOPS ROBUSTUS

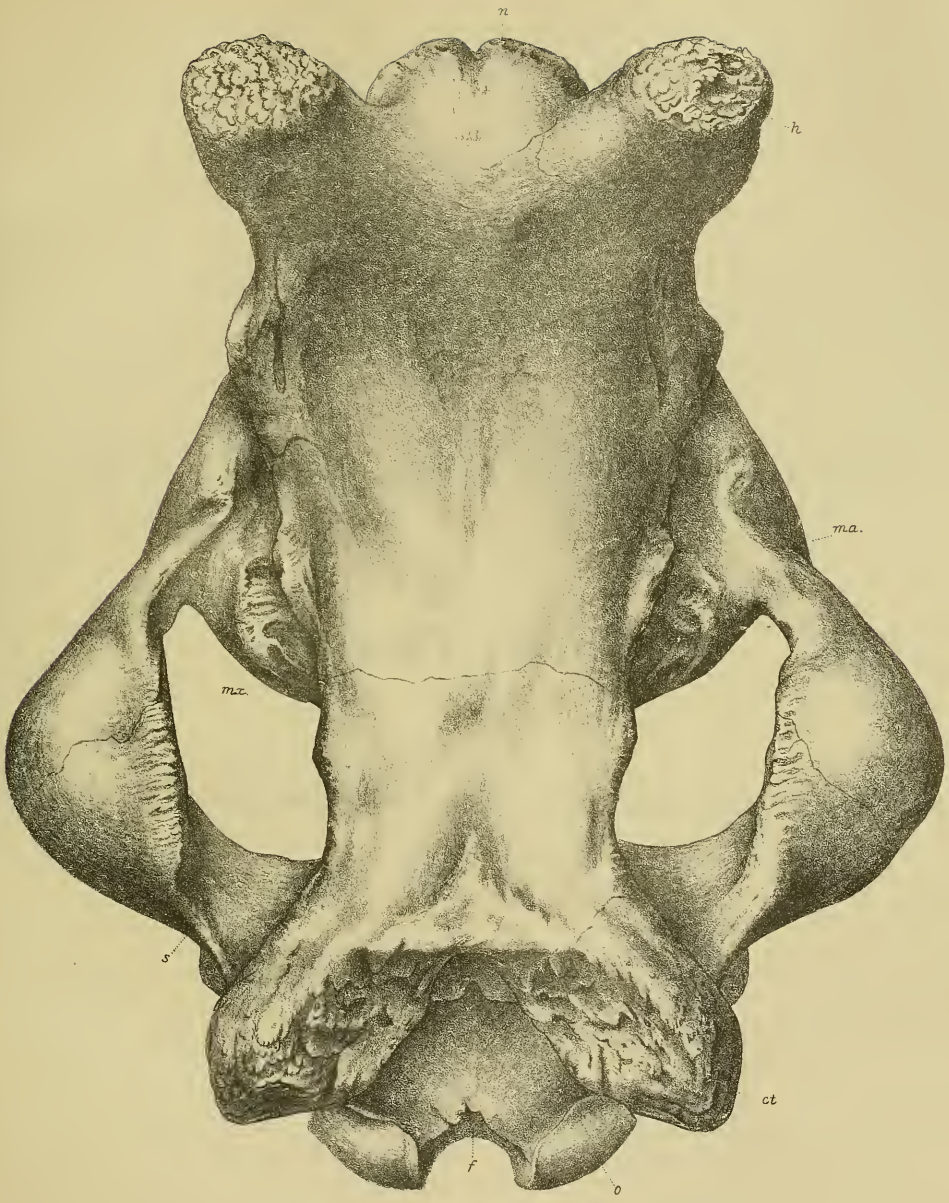
PLATE XCVIII

PLATE XCVIII

Type Skull of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 494, also Pls. XCVI and XCVII)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. The top view shows well the extreme breadth of the skull as compared with that of *B. dispar* (Pl. XCI). In *Brontotherium* the skull top is much longer, the occipital vertex is produced backward, and there is little or no constriction of the vertex in front of the occiput.



TYPE SKULL OF BRONTOPS ROBUSTUS

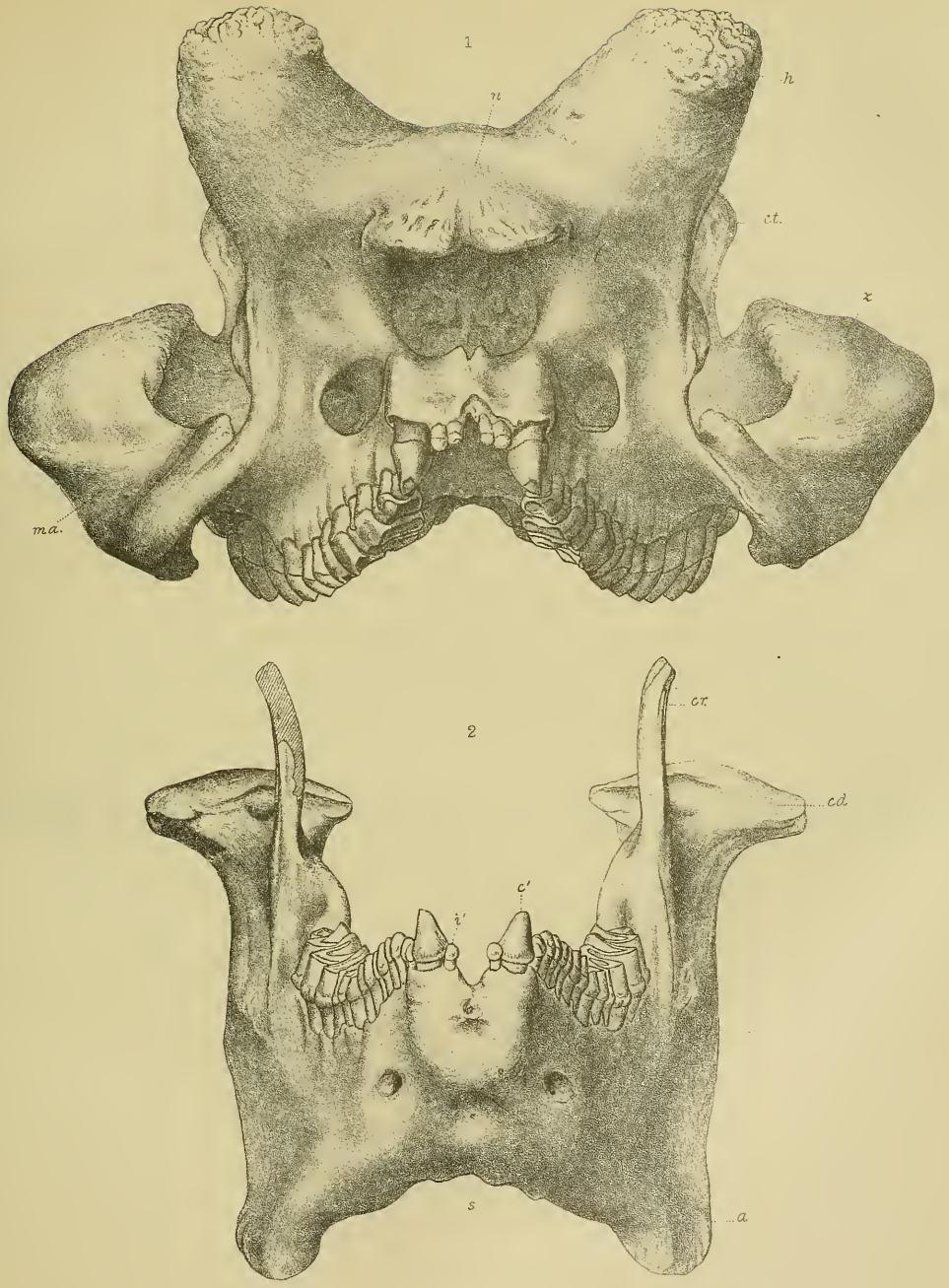
PLATE XCIX

PLATE XCIX

Type Skull and Jaw of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 494, also Pls. XCVI–XCVIII)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. The front view of the skull, compared with that of *Brontops dispar* (Pl. XCIV), shows the increased specialization in its greater size and width, expanded zygomata, and thickened horns.



TYPE SKULL AND JAW OF BRONTOPS ROBUSTUS

PLATE C

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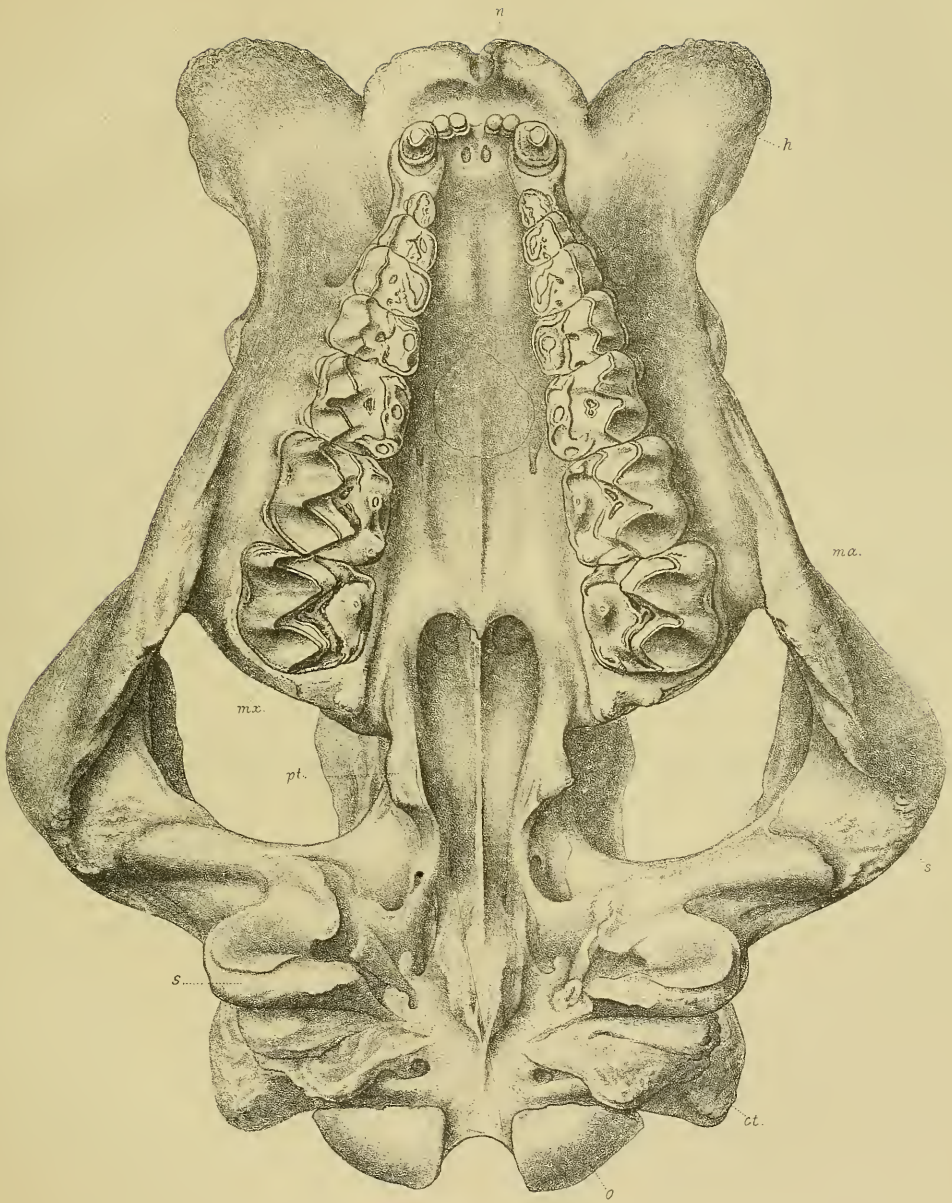
PLATE C

Type Skull of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 494)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. The palatal view shows well the extreme breadth, which is characteristic of this species. The dentition is shown also in Plate CI.



TYPE SKULL OF BRONTOPS ROBUSTUS

PLATE CI

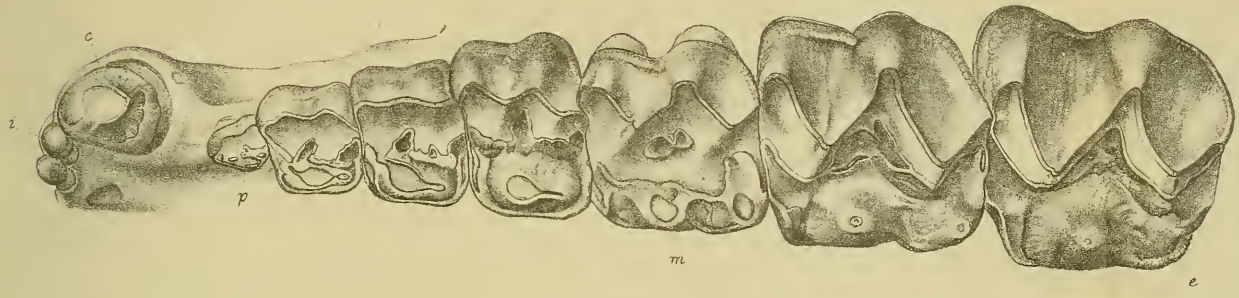
PLATE CI

Dentition of Type Skull of Brontops robustus

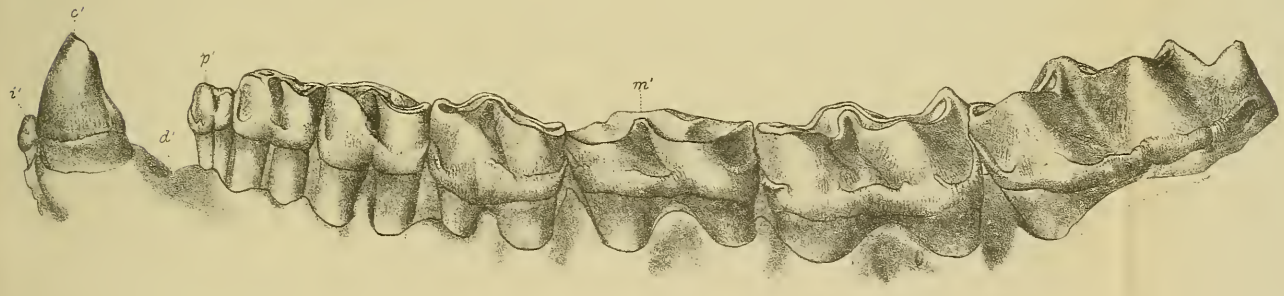
Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 495.)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. The upper teeth (B_1, B_2) may be compared with those of *B. dispar* (Pl. LXXXVIII). In *B. robustus* the internal cingula of the premolars are somewhat reduced, but the postero-internal cusps or tetartocones are better developed. There is also a wide postcanine diastema. Although the canines suggest those of *Brontotherium* (Pl. CLXIII) the incisors are not broadly cingulate posteriorly, as in that genus; the tetartocones, especially in p^4, are more retarded; p^4 is also less molariform than in *Brontotherium;* and all the cheek teeth are narrower transversely. The lower teeth (A_1, A_2) show reduced external cingula on the premolars and molars.

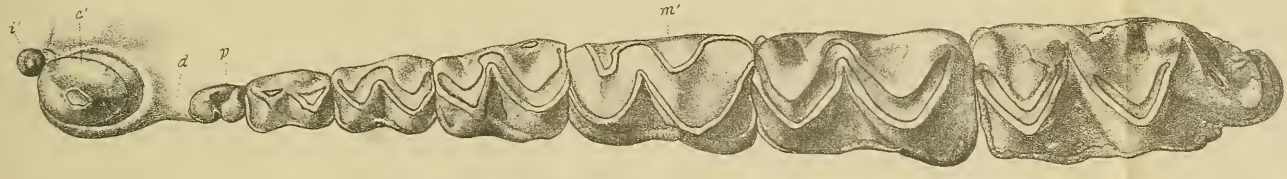
B2



B1



A2



A1

DENTITION OF TYPE SKULL OF BRONTOPS ROBUSTUS

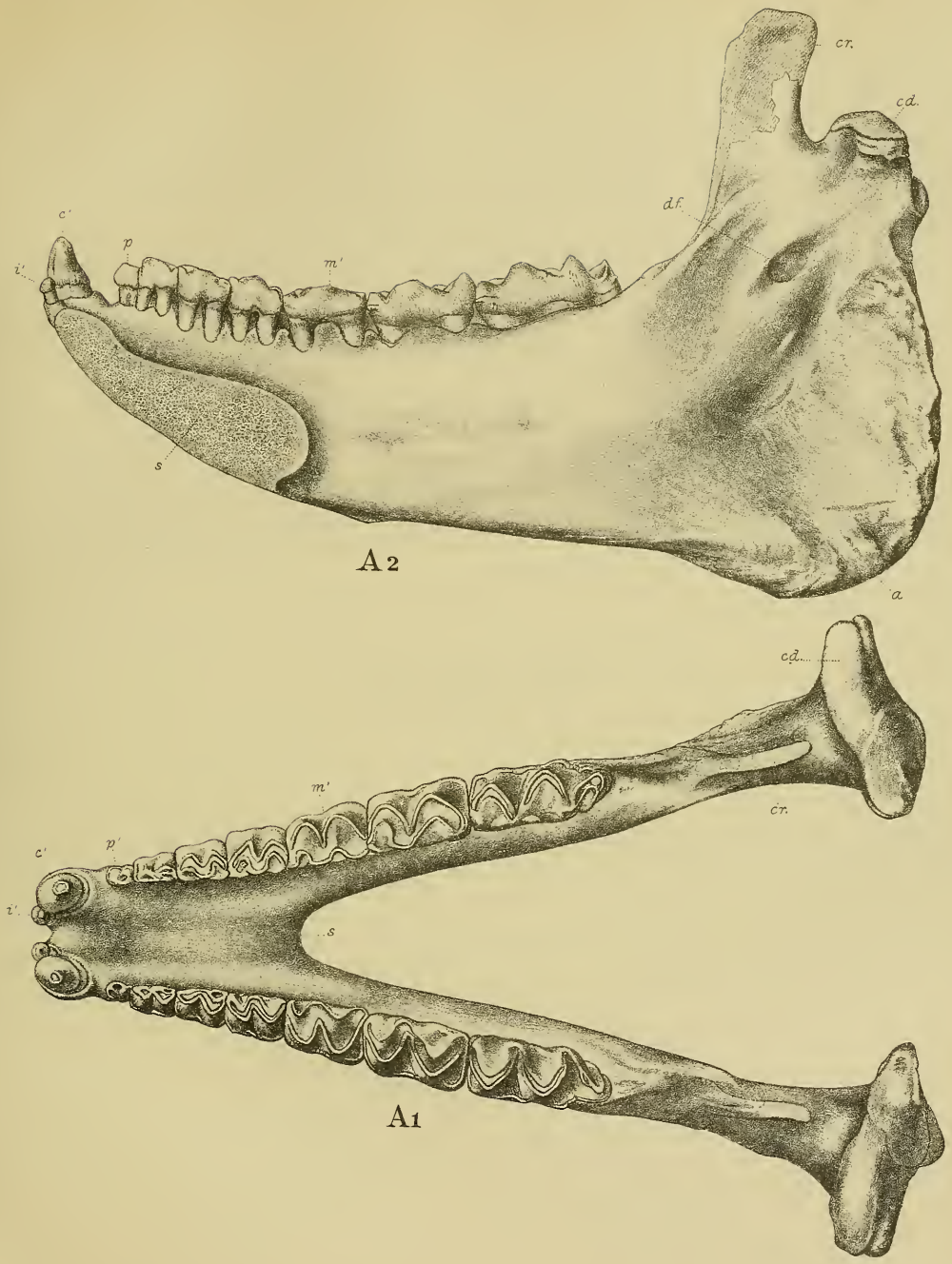
PLATE CII

PLATE CII

Lower Jaw of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 496)

Yale Mus. 12048, type, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. A_1, Top view; A_2, side view. The very shallow symphyseal region of this jaw by convergent evolution resembles that of *Brontotherium*.



LOWER JAW OF BRONTOPS ROBUSTUS

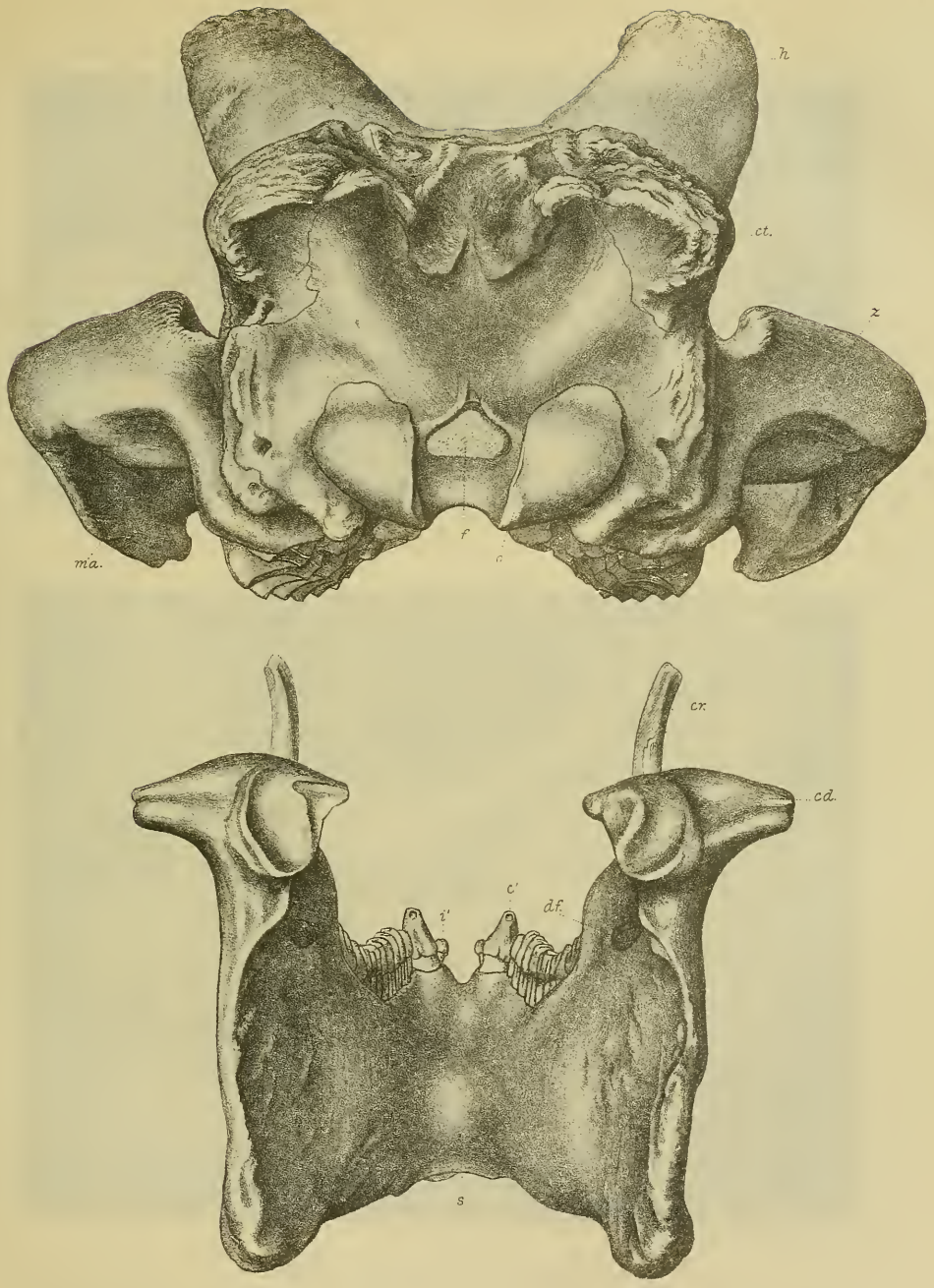
PLATE CIII

PLATE CIII

Type Skull and Jaw of Brontops robustus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 494)

Yale Mus. 12048, Dry Creek, 5 miles northeast of Chadron, Nebr. (J. B. Hatcher), Chadron formation, probably upper levels. Posterior view of skull and jaw, illustrating the great breadth of the skull, the deep fossae for the attachment of the heavy neck muscles, and the transversely expanded condyle of the jaw.



TYPE SKULL AND JAW OF BRONTOPS ROBUSTUS

A^2

A^1

TYPE SKULL OF DIPLOCLONUS BICORNUTUS

One-fifth natural size. (See p. 501.) Am. Mus. 1476, Quinn Draw, Big Badlands, S. Dak., Chadron formation. This skull is referred to the genus *Diploclonus* from the presence of an accessory knob or hornlet on the antero-internal face of the horn. It differs from *Diploclonus amplus* in the smaller size of the horns and in the lesser width of the zygomata (the narrowness of the skull is emphasized by lateral crushing). The side view (A^1) shows the characteristics of the menodontine group (deeply concave skull top, long stout nasals, grinding teeth with sharp external cingula). The top view (A^2) suggests that of *Menodus*. This skull was at first regarded as that of a female, but the stout canines and zygomata do not support this view

PLATE CV

PLATE CV

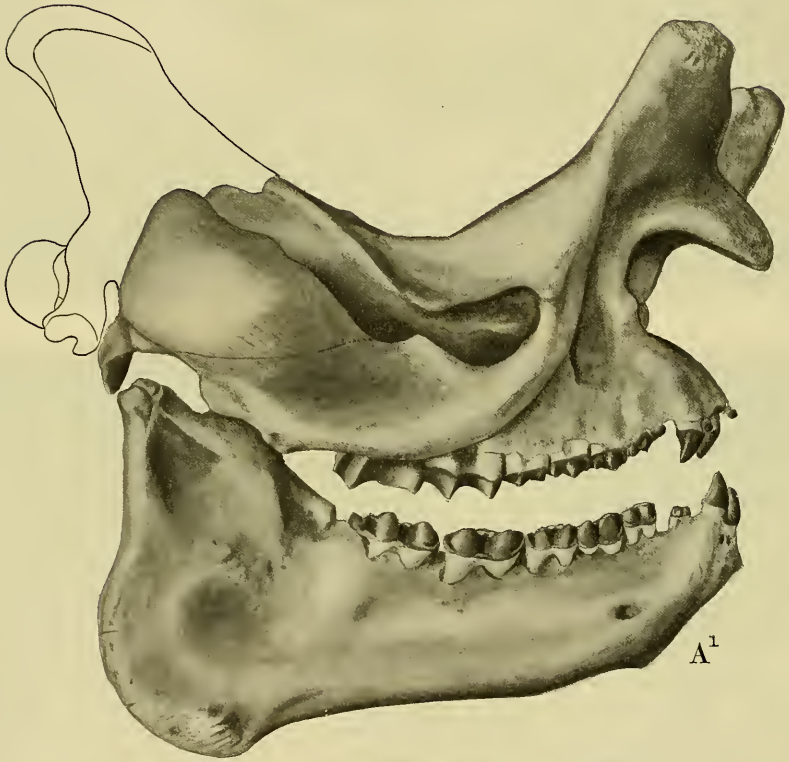
Skull Related to Diploclonus tyleri

Am. Mus. 1081, original paratype (see p. 502) of *D. bicornutus* Osborn, Cheyenne River, S. Dak., Chadron formation. A^1, Side view; A^2, top view. One-fifth natural size. This skull was at first regarded by Osborn as a male of *D. bicornutus*, but, as observed by Lull, its closer resemblances are with the type of *D. tyleri*. (See Pl. CVII.) It approaches the type of *D. amplus* in breadth, but the horns are not so flat. The accessory hornlets are well marked. The length of the nasals is conjectural. The constricted parietal region and very concave skull top are characteristic of the menodontine group. The longitudinal slit in the parietal vertex is in the region of the sagittal fossa of *Manteoceras* and of a parietal opening in certain skulls of *Brontops brachycephalus;* apparently the outer tabula of the parietal bone was thin in this region. Irregular projections of the temporal crest above the mid-cranial region are seen, as in *Allops*, and they may have marked the dorsal edge of the insertion area for the temporal muscle.

A¹

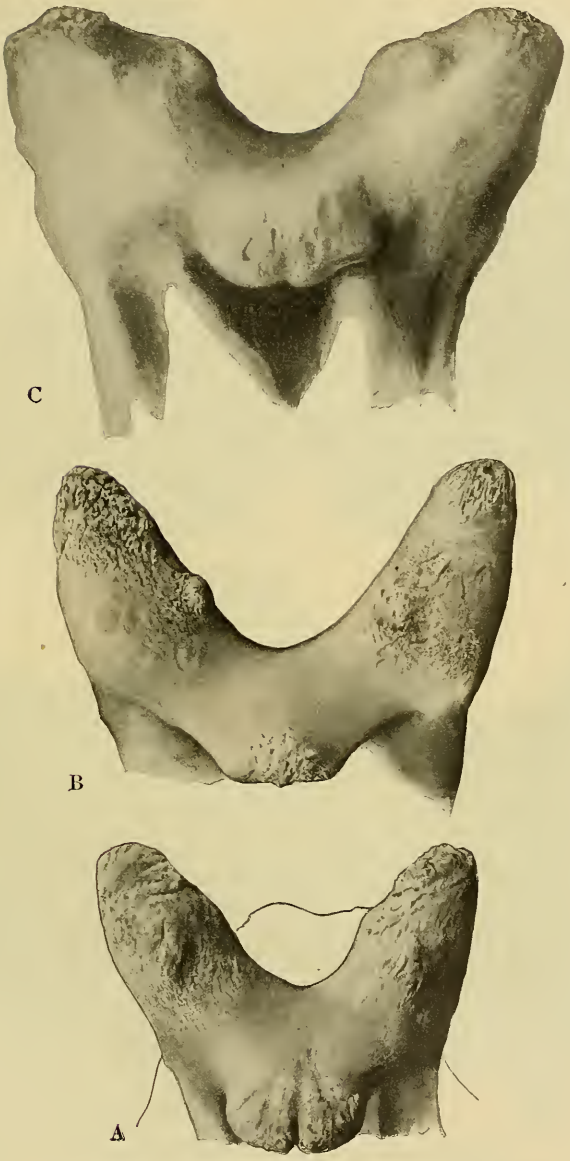
A²

SKULL RELATED TO DIPLOCLONUS TYLERI



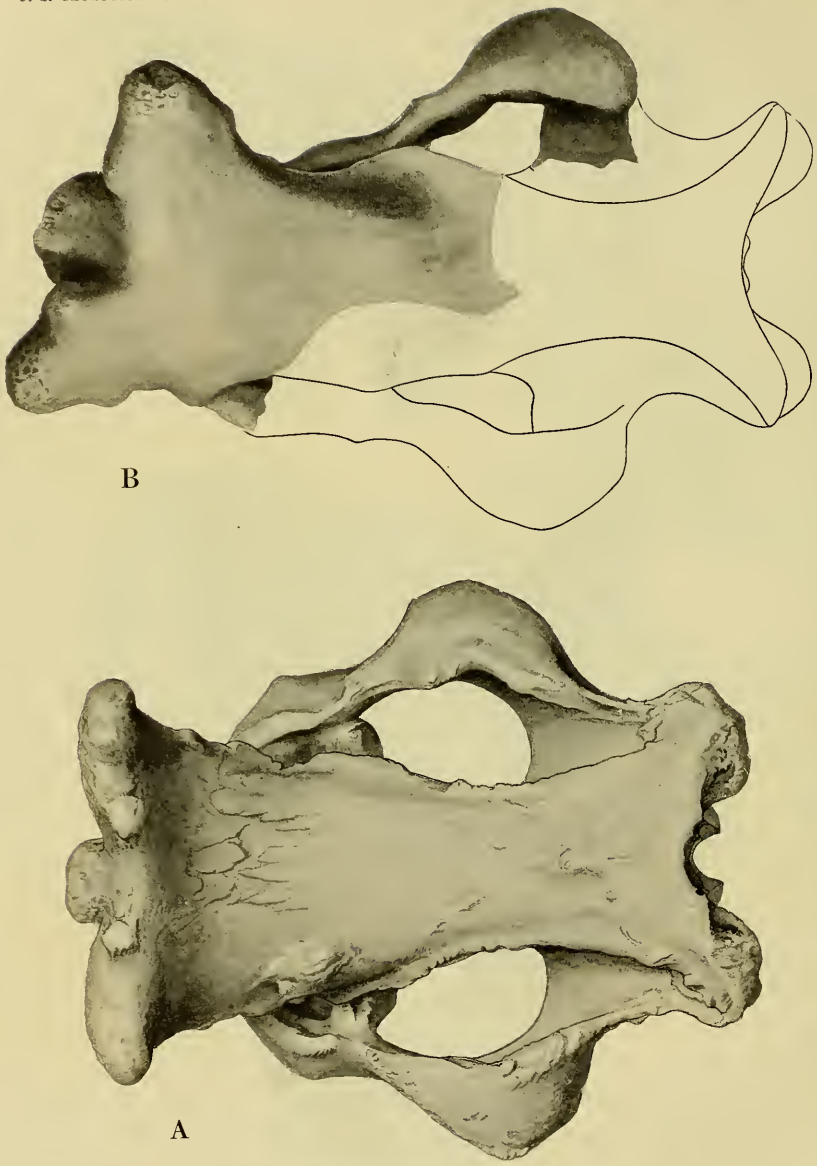
TYPE SKULL, JAW, AND TEETH OF DIPLOCLONUS TYLERI

After original figures by Prof. R. S. Lull. (See p. 503.) One-sixth natural size. Amherst College Zool. Coll. 327, type, "near the head of Bear Creek, a tributary of the Cheyenne River [S. Dak.]. The exact locality was on the north side of Spring Draw Basin, about 10 miles from the mouth of Bear Creek. Here some 200 feet of titanothere beds were found, lying upon Fort Pierre deposits, in which titanothere bones were discovered from a point 6 feet above the contact upward; the specimen under consideration lying 35 feet above the base of the beds, hence in the upper part of the lower division."—J. B. Hatcher, Am. Naturalist, vol. 27, p. 218, 1893, cited by R. S. Lull, 1905, p. 443. This large skull recalls *Brontops robustus* or a progressive B. *dispar* in general appearance but is referred to the subgenus *Diploclonus* partly because it has a large accessory hornlet. The canine is very stout; in p^4 there is practically but one internal cusp, the postero-internal cusp being barely defined and continuous with the cingulum. The general pattern of the premolars is the same as in *Allops* and *Brontops*. The lower jaw recalls that of *Brontops robustus*. (See Pls. XCVII, XCIX, and CII)



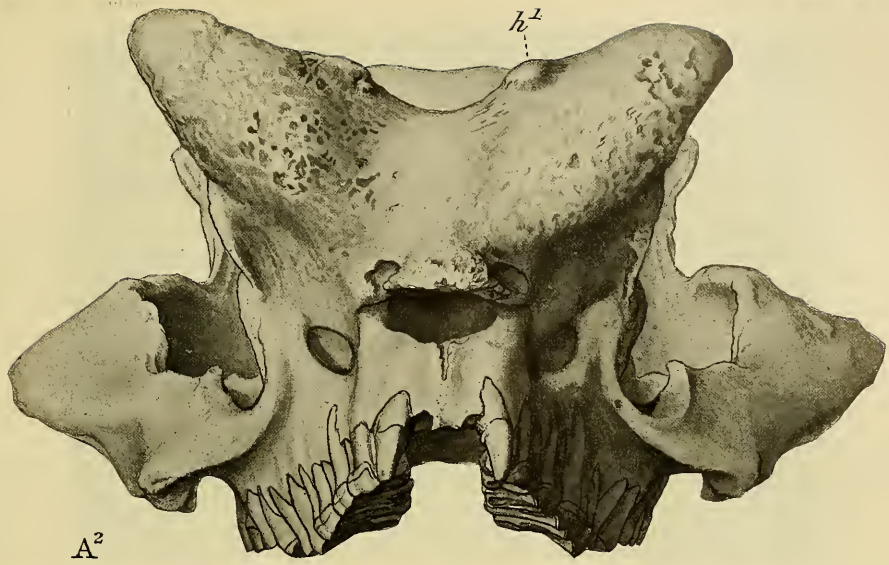
NASOFRONTAL REGION OF SKULLS OF DIPLOCLONUS

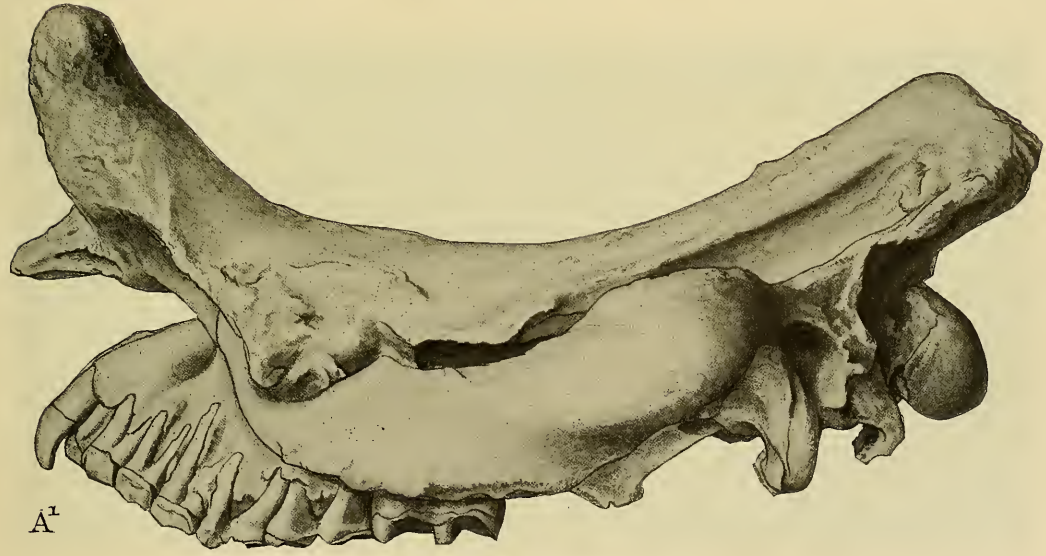
A, *D. bicornutus*, type (Am. Mus. 1476). B, *D. tyleri*(?), referred (Am. Mus. 1081); the nasals are largely restored. C, *D. tyleri*, type (Amherst College Zool. Coll. 327; after Lull). In these skulls we observe a progressive enlargement and widening of the horns, which culminates in *D. amplus*. (See pp. 501, 503, also Pls. CIV, CV, and CVI)



TYPE SKULLS OF DIPLOCLONUS AMPLUS AND D. TYLERI

One-sixth natural size. (See pp. 503, 504, also Pls. CVI and CIX.) A, *Diploclonus amplus*, type (Yale Mus. 12015a), South Dakota, Chadron formation. Figure prepared under the direction of Professor Marsh. This view exhibits well the pronounced brachycephaly, the flattening of the horns, the prominent hornlets, and the abbreviation of the nasals. (See Pl. CVII.) B, *D. tyleri*, type (Amherst College Zool. Coll. 327), near the head of Bear Creek, a tributary of Cheyenne River, S. Dak., Chadron formation. (After R. S. Lull.) In the top view this skull approaches *D. amplus*





TYPE SKULL OF DIPLOCLONUS AMPLUS

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 504.) Yale Mus. 12015a, type, South Dakota, Chadron formation. The lateral view (A1) exhibits well the concave skull top, stout zygomata, thick, pointed horns, and short nasals. The form of the canine recalls that of *Allops* and of *Menodus*; the upper premolars have external cingula. In front view (A2) the pointed horns, pronounced hornlets, and wide zygomata are especially noteworthy. (Compare Pl. CVII)

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A_2

A_1

SKULL REFERRED TO DIPLOCLONUS AMPLUS?

Nat. Mus. 4710, skull e, Indian Draw, Big Badlands, S. Dak., Chadron formation (in 1901 Mr. Hatcher did not recall the exact level). One-fourth natural size. (See p. 505.) This skull is provisionally regarded as the female of *D. amplus*, although its canines seem hardly small enough to support this view. As compared with the type of *D. amplus* the zygomatic swellings and horns are much less developed

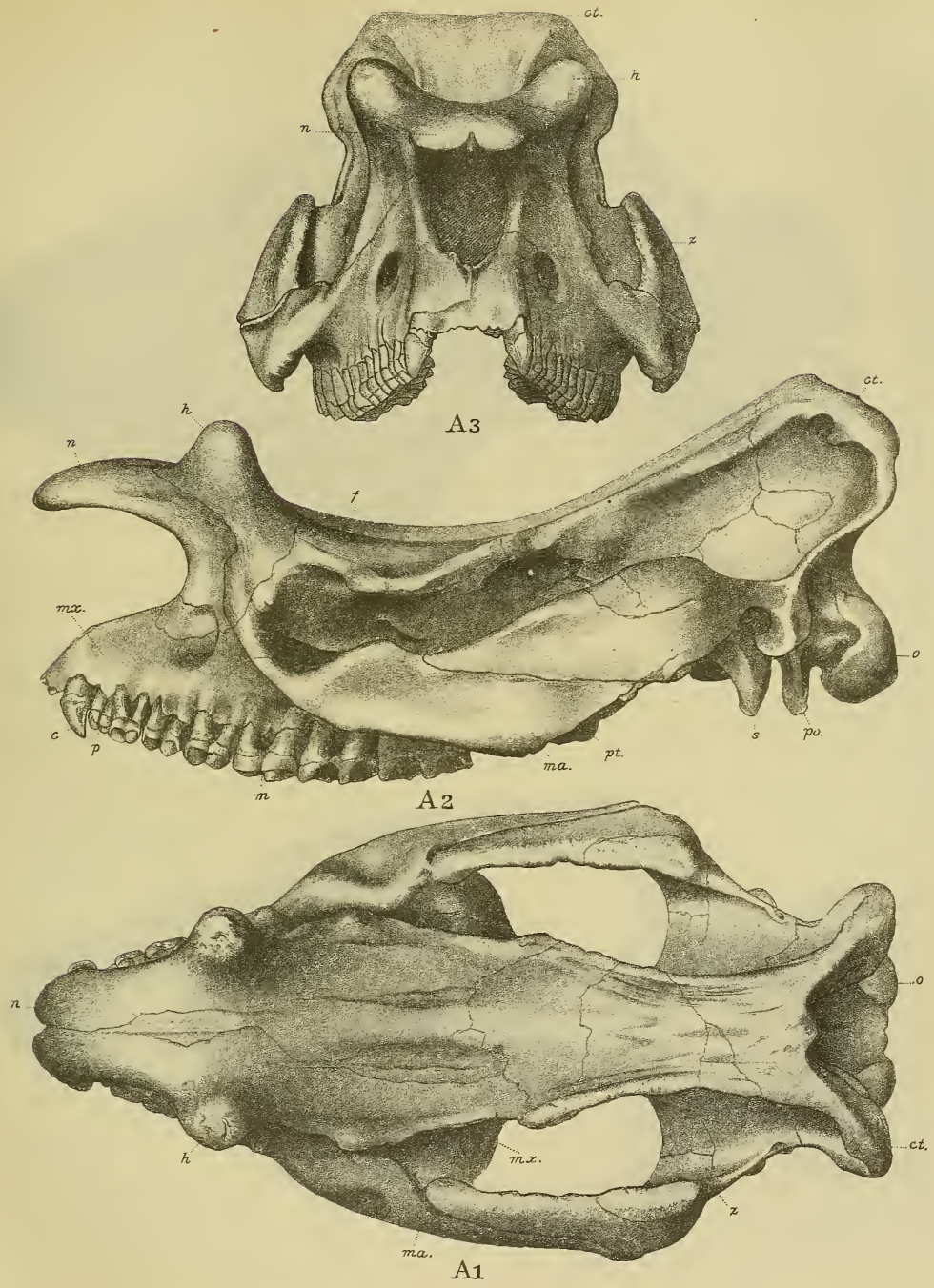
PLATE CXI

PLATE CXI

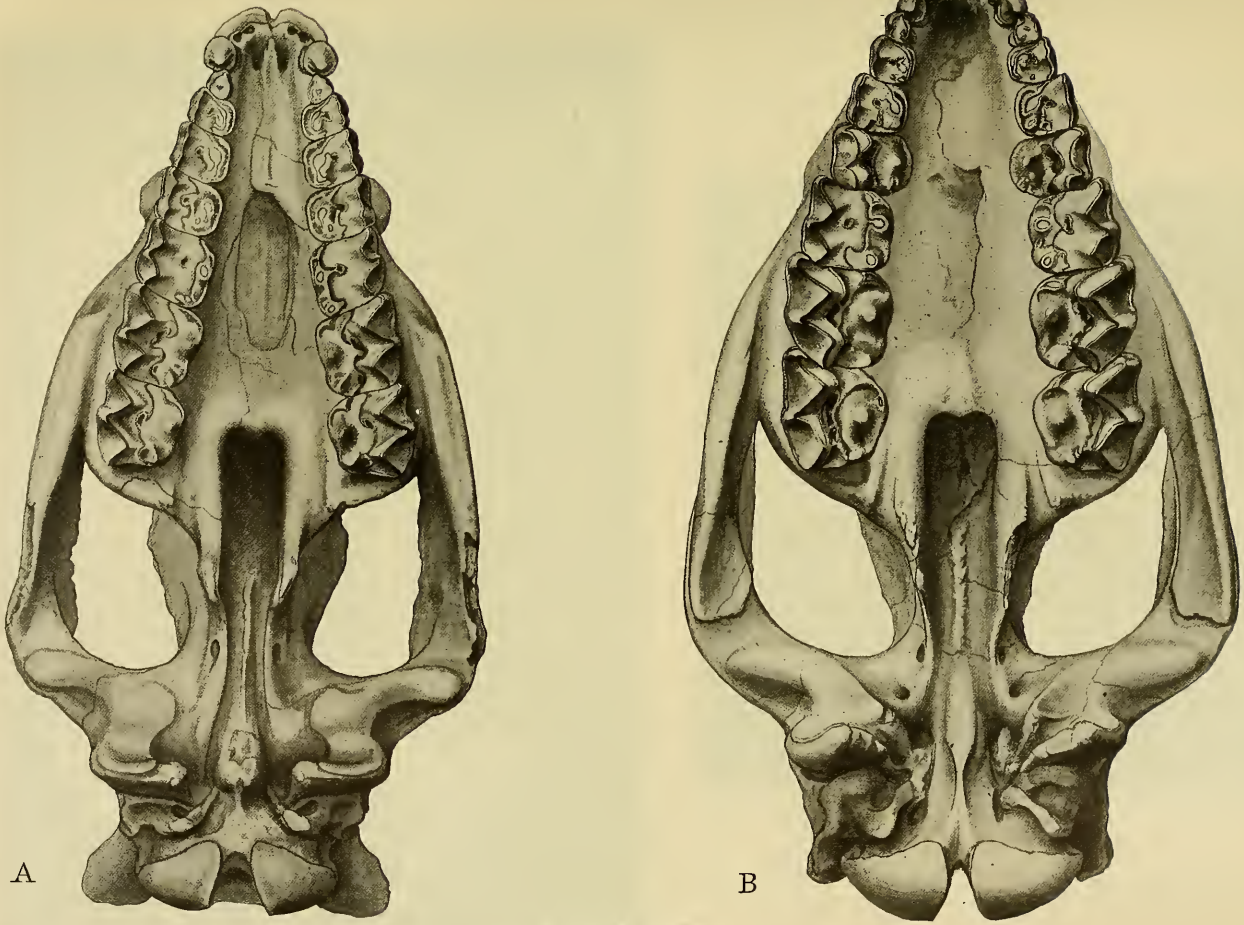
Type Skull of Allops walcotti

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 509)

Nat. Mus. 4260, skull Q, type, South Dakota, probably Corral Draw, *Titanotherium* zone, lower levels (J. B. Hatcher). This is regarded as the most primitive *Allops*. The specimen, which is badly crushed laterally, was at first referred by Osborn to *Menodus heloceras*, but it differs from *Menodus* in the more elongate oval section of the horns and the more tapering form of the nasal and in the facts that two distinct incisor alveoli are retained and that the canines are compressed anteroposteriorly. It is therefore considered a very primitive member of the *Allops* phylum. The species shares much in common with *Menodus heloceras* (dolichocephaly, elongate grinders, sharp internal and external cingula, etc.) and according to the "group method" of classification would be placed in a primitive genus ancestral to both *Menodus* and *Allops*.



TYPE SKULL OF ALLOPS WALCOTTI



SKULLS OF ALLOPS

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See pp. 508, 509.) A, *Allops walcotti*, skull Q, type (Nat. Mus. 4260), South Dakota, probably Corral Draw, *Titanotherium* zone, lower levels (J. B. Hatcher). A more accurate drawing of the premolars is given in Plate CXI. Noteworthy features are the large incisive alveoli, the elongation of the grinding teeth, and their small size as compared with those of *Allops marshi* (cf. B). There is a strong general resemblance to *Menodus heloceras*. B, *Allops? marshi*, skull J, referred (Nat. Mus. 4738), Hat Creek, Nebr., *Titanotherium* zone, level probably lower B (J. B. Hatcher). Marked contrast to *Allops walcotti* is shown in the greater width of the skull, in the large size of the grinding teeth, and in the peculiar character of p^4, all indicating a more advanced stage of this phylum

A^2

A^1

SKULL OF ALLOPS MARSHI?

Field Mus. P6900. A_1, Side view; A_2, front view. One-fourth natural size. (See p. 508.) This finely preserved skull and lower jaw are somewhat smaller than the type of *Allops walcotti*. The species is more brachycephalic than *Brontops brachycephalus* and has smaller horns than the typical *Allops*. The relatively large canines indicate that the specimen is a male and not a female of some larger animal. There is a large incisor in the lower jaw. In general this specimen seems nearest to *Allops marshi*, although the horns are smaller

PLATE CXIV

PLATE CXIV

Skulls of Allops marshi

One-fifth natural size. (See pp. 508, 512, 513)

A, Am. Mus. 1445, paratype, Cheyenne River, S. Dak., Chadron formation. Crushing from above has lessened the vertical diameters of this skull. It is more massive than the type skull and less massive than that of *Brontops dispar*.

B, British Mus. 4446M. This well-preserved skull differs from the type chiefly in the greater elevation of the occiput, accenting the deeply concave upper profile characteristic of all Menodontinae. The dental measurements are given on page 508.

C, Am. Mus. 501, type, South Dakota, probably Cheyenne River Badlands, Chadron formation. This specimen was at first placed in the genus *Brontops* near *B. brachycephalus* and *B. dispar*. It is, however, less brachycephalic, its horns have a trihedral basal section, the canine is compressed anteroposteriorly, and the premolars and molars are of moderate breadth, with internal and external cingula. This combination of characters is seen only in the genus *Allops*, and the upper premolars of the present specimen closely resemble those of *Allops serotinus*. The upward pitch of the nasals is due to crushing.

C

B

A

SKULLS OF ALLOPS MARSHI

PLATE CXV

PLATE CXV

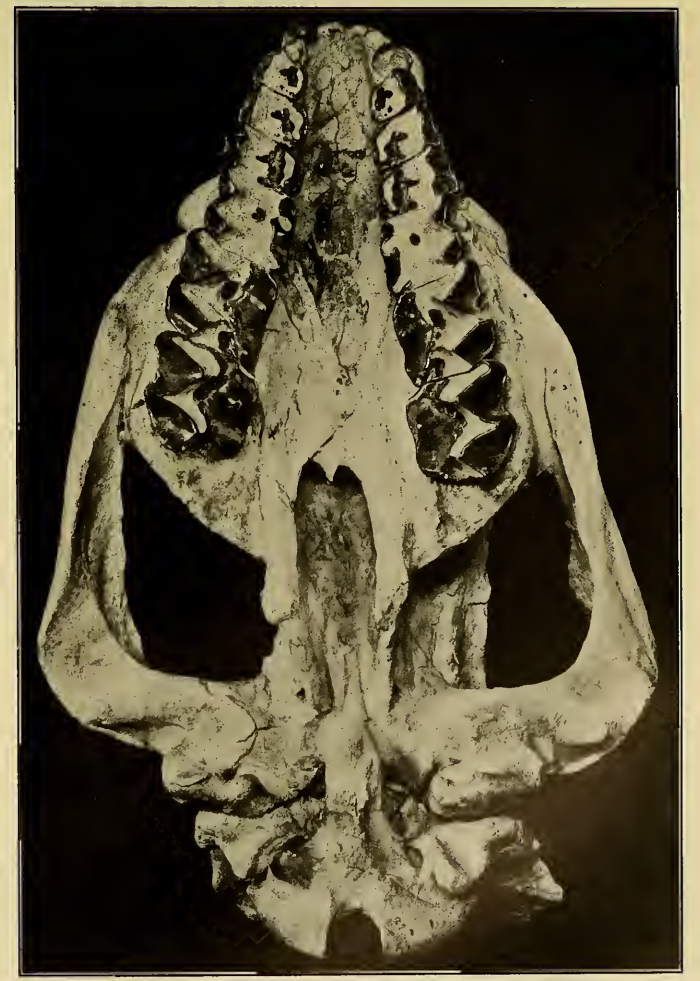
Skulls of Allops marshi

One-fourth natural size. (See pp. 512, 513)

A, Am. Mus. 1445, paratype, Cheyenne River, S. Dak., Chadron formation. This skull is more brachycephalic than the type, but less so than in *Brontops dispar*. The width across the horns foreshadows *Allops crassicornis*. The constricted parietal region is characteristic of all the Menodontinae.

B, Am. Mus. 501, type; South Dakota, probably Cheyenne River Badlands, Chadron formation. The skull is slightly crushed in the left side anteriorly. The canine is compressed anteroposteriorly, the grinding teeth are of moderate width, with marked internal and external cingula. The premolars have deep medifossettes, as in *Menodus*, and closely resemble those of *Allops serotinus*. The well-preserved basicranial region shows well the fossa for the internal extension of the interarticular disk and the structures in the region of the periotic.

←A



B

SKULLS OF ALLOPS MARSHI

PLATE CXVI

PLATE CXVI

Skulls of Allops marshi?

One-fifth natural size. (See p. 514)

A, Nat. Mus. 1213, skull E, Big Cottonwood Creek, Nebr., *Titanotherium* zone, level A 2 (J. B. Hatcher). (If this is skull E of the 1887 collection, the locality is as given; if it is skull E of the 1886 collection, the locality is uncertain.) This specimen has small horns and weak zygomata and is probably a female. The grinding teeth are relatively broader than in the type skull and suggest those of *B. dispar*.

B, Nat. Mus. 1215, skull A[1]. This subbrachycephalic skull recalls that of *Brontops brachycephalus*. Its reference to *Allops marshi* appears somewhat doubtful.

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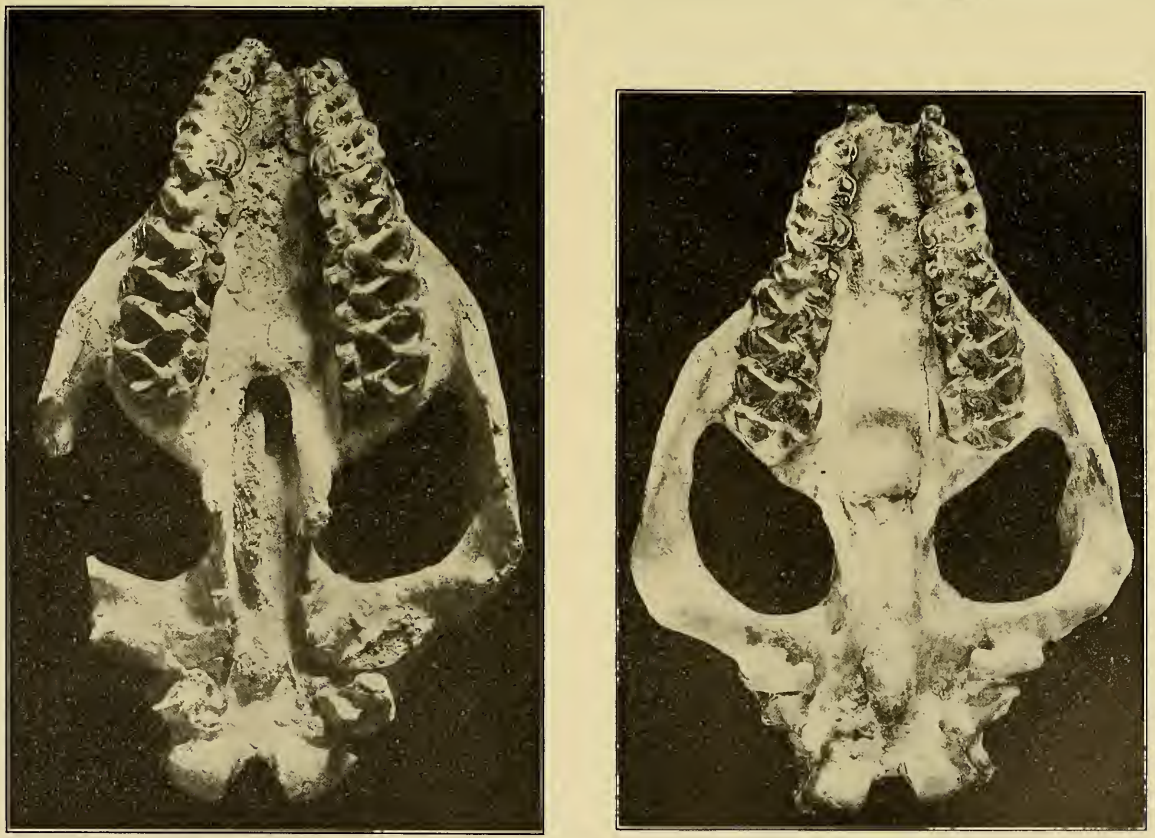


A B

SKULLS OF ALLOPS MARSHI?

PLATE CXVII

PLATE CXVII

Skulls of Allops serotinus

One-seventh natural size. (See pp. 515, 516, 517, also Pls. CXIX and CXX)

A, Nat. Mus. 4251, skull H, type, Big Badlands, S. Dak., *Titanotherium* zone, level C (J. B. Hatcher).[1] The horns are widely divergent, trihedral in basal section; the connecting crest lies in the posterior plane of the horns; the nasals are abbreviated by the forward growth of the horns; the parietal region is narrow, the zygomatic expansion moderate, the skull top long, the occiput produced backward.

B, Am. Mus. 520, Cheyenne River, S. Dak., Chadron formation. A skull referred to *A. serotinus* in which the above-mentioned features are emphasized.

C, Nat. Mus. 4938, skull j, Big Badlands, probably Indian Draw, S. Dak., *Titanotherium* zone, level middle C (J. B. Hatcher). A skull referred to *A. serotinus*. The horns and nasals are more massive than in the preceding specimen, and the parietal crest is broader.

D, Nat. Mus. 2151, skull I, collection of 1886, Big Badlands, S. Dak., Chadron formation, level upper C, 80 feet above Pierre shale (J. B. Hatcher). Skull of a supposed female with small horns and slender zygomata, referred to *A. serotinus*.

[1] Hatcher says, "77 feet above Fort Pierre shale; 34 feet below base of *Oreodon* beds, allowing liberally for summit of *Titanotherium* beds." Darton (in letter) gives 40.7 feet above Pierre shale for the same skull H.

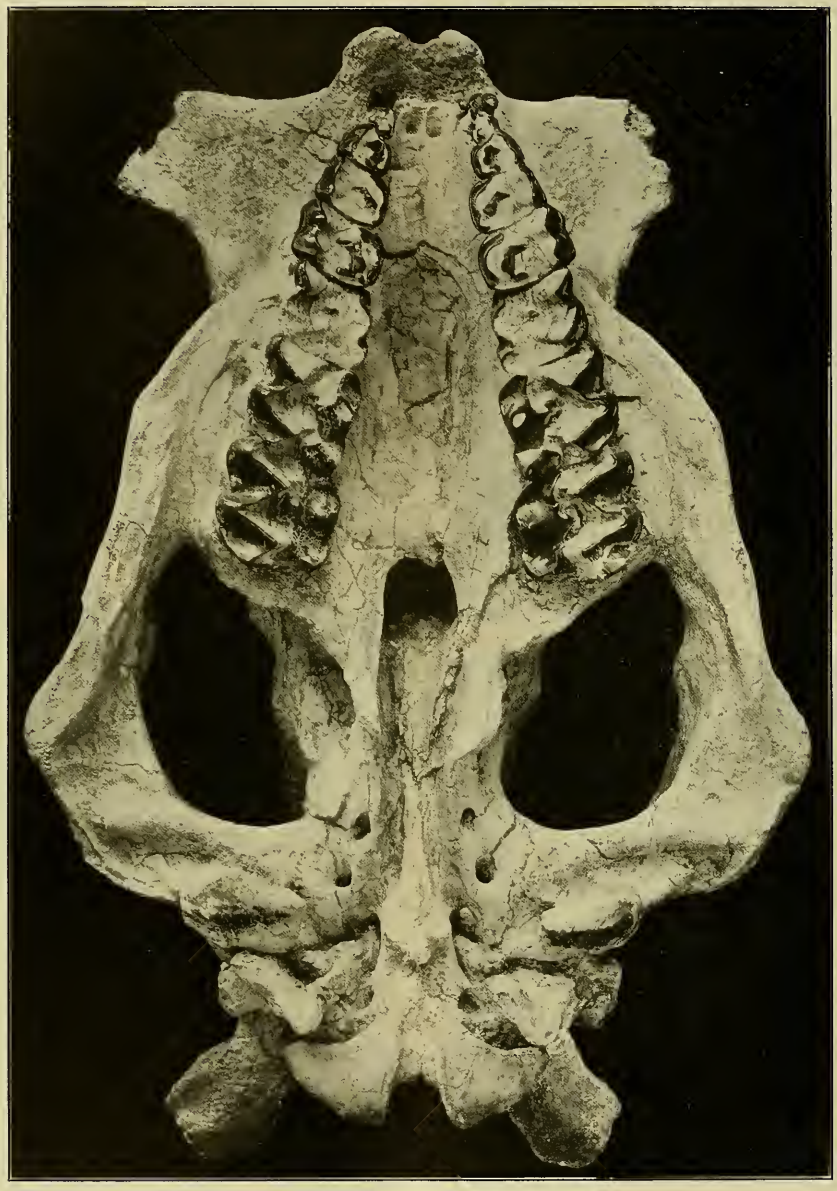
C

D

A

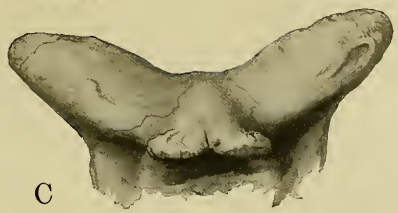
B

SKULLS OF ALLOPS SEROTINUS

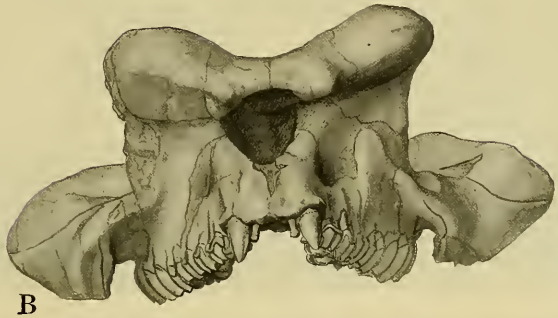


SKULL OF ALLOPS SEROTINUS

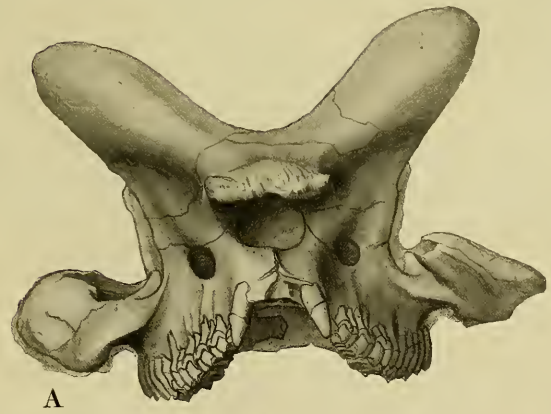
Am. Mus. 520, Cheyenne River Badlands, S. Dak., Chadron formation. One-fourth natural size. (See p. 517, also Pl. CXVII.) A skull referred to *Allops serotinus*. The generic characters of *Allops* which are seen in this view are as follows: Incisors 2–1, canines compressed anteroposteriorly, premolars with sharp external and internal cingula, grinding teeth and skull of moderate breadth, zygomatic expansion moderate, horns widely divergent. The reference of this specimen to *A. serotinus* is based especially on the detailed resemblances in the premolars to those of the referred skull Nat. Mus. 4938 (Pl. CXX, B). The postero-internal cusps of the premolars are less developed than in *A. crassicornis*



C



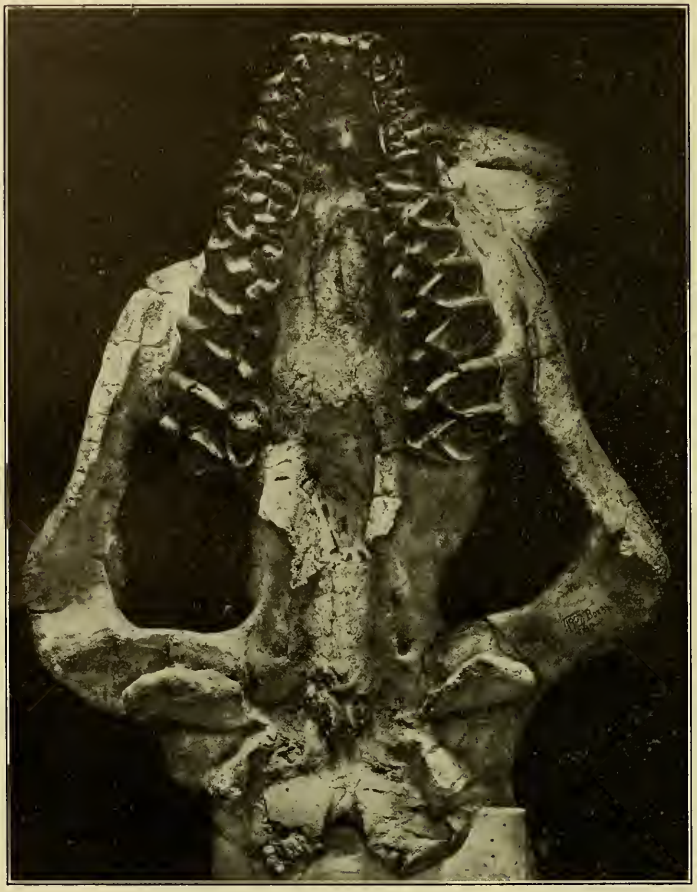
B



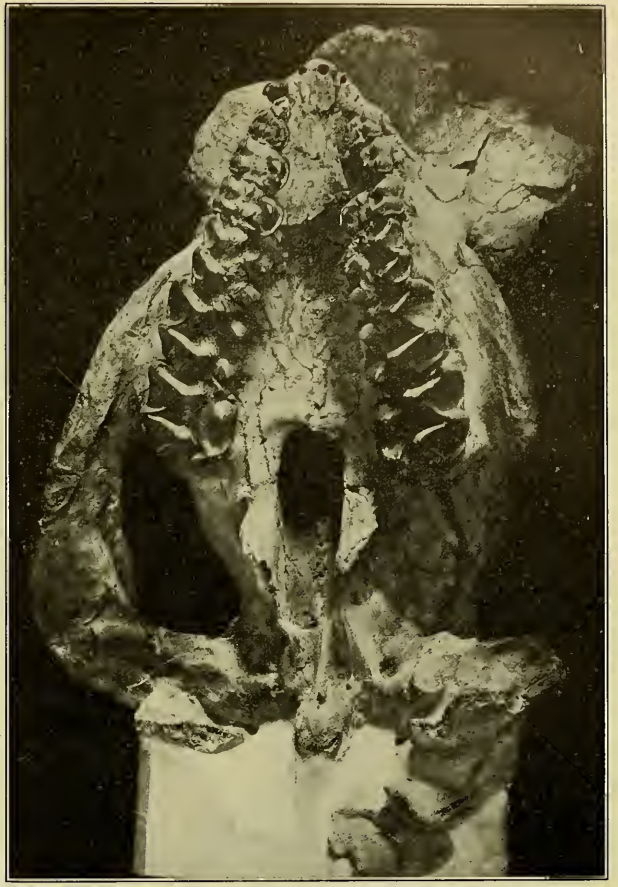
A

FRONT VIEWS OF SKULLS OF ALLOPS

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See pp. 515, 517.) A, *Allops serotinus*, skull H, collection of 1886, type (Nat. Mus. 4251), South Dakota, Chadron formation, level C. The front view shows well the long, widely divergent horns, thick nasals, and moderately expanded zygomata, which are characteristic of this species. B, *Allops crassicornis*, skull Z^1, collection of 1888, type (Nat. Mus. 4289), South Dakota, Chadron formation, level lower C (in Hatcher's tabular list of skulls; later (1901) he was "inclined to place this higher up"). In this species the horns are thicker and the zygomata more massive than in *A. serotinus*. C, *Allops serotinus*, skull J^1, referred (Nat. Mus. 4945), Big Badlands, S. Dak., Chadron formation, level not listed. The horns are more pointed at the tip than in other specimens of *Allops*



A



B

SKULLS OF ALLOPS CRASSICORNIS AND A. SEROTINUS

One-fifth natural size. (See p. 517, also Pls. CXVII and CXIX.) A, *Allops crassicornis*, skull Z^1, type (Nat. Mus. 4289), Big Badlands, S. Dak., Chadron formation, level lower C (Hatcher). The skull is of moderate width, less brachycephalic than in *Brontops*, less dolichocephalic than in *Menodus*. There is a single incisor on each side, the canine is compressed anteroposteriorly, the premolars have sharp external and internal cingula, and the molars are of moderate breadth. Specific differences from *Allops serotinus* (B) are shown in the higher development of the postero-internal cusps of the premolars. B, Skull referred to *Allops serotinus*, skull *j* (Nat. Mus. 4938), Big Badlands, S. Dak., probably Indian Draw, *Titanotherium* zone, level middle C (Hatcher). The nasals and horns are very massive and the zygomata deep. The postero-internal cones of the premolars are retarded. The molars are fairly broad

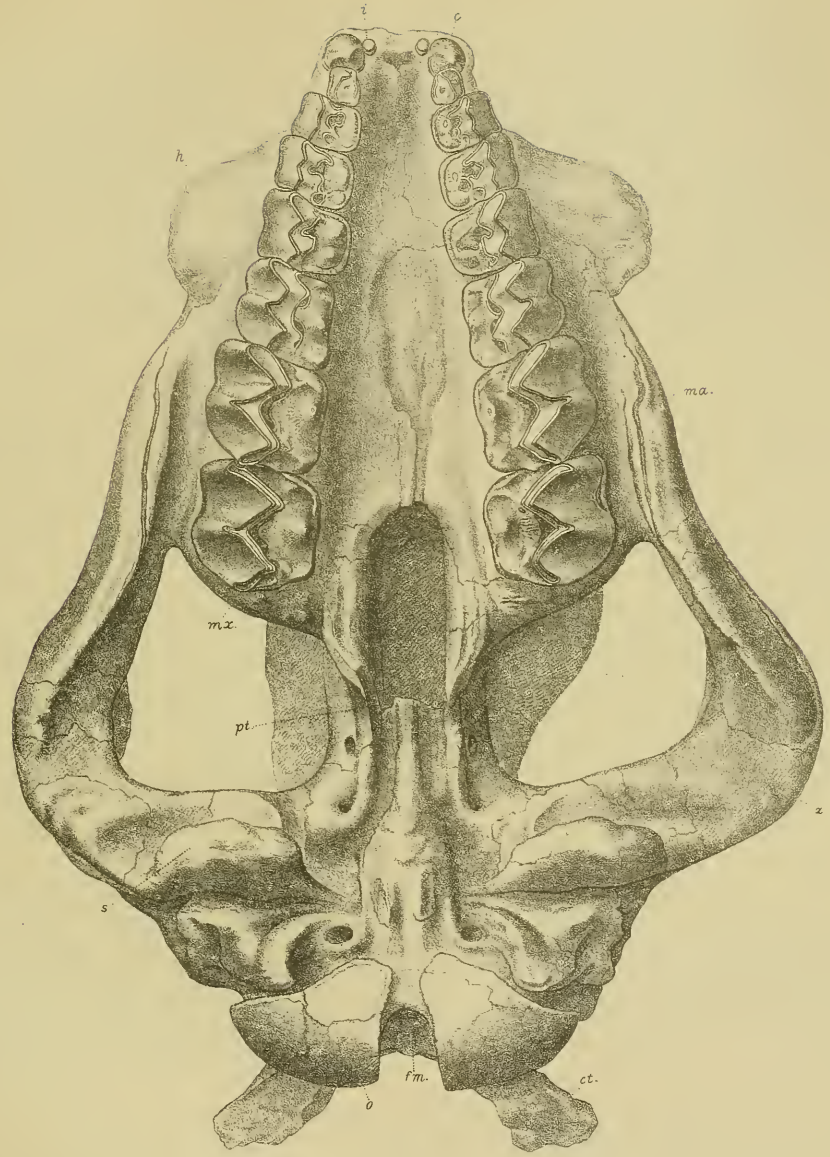
PLATE CXXI

PLATE CXXI

Type Skull of Allops crassicornis

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 517)

Nat. Mus. 4289, skull Z¹, type, Big Badlands, S. Dak., Chadron formation, level lower C. A photograph of the specimen as it actually appears in the crushed condition is shown in Plate CXX, A. The aspect of the skull in this plate illustrates the mingling of *Brontops* and *Menodus* characters seen in this genus.



TYPE SKULL OF ALLOPS CRASSICORNIS

PLATE CXXII

PLATE CXXII

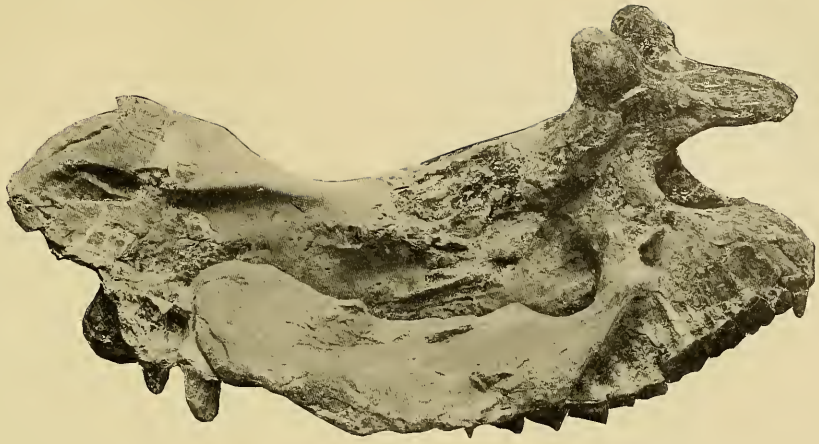
Skull, Jaw, and Teeth of Allops crassicornis? seu marshi

A^1, Skull, right side; A^2, right upper dentition; B^1, lower jaw, inner view of left half; B^2, lower dentition, crown view. Figures of skull one-fifth natural size; figures of teeth one-half natural size. (See p. 508.)

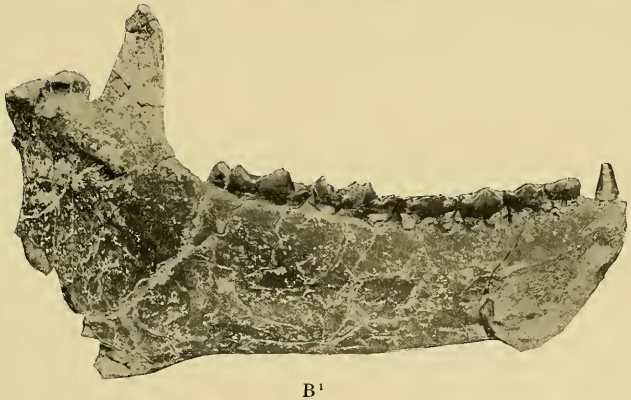
British Mus. 5743M, female skull and jaws referred to *Allops crassicornis?*, one individual. The premolar pattern is essentially identical with that of the type *A. crassicornis*, although the resemblance is obscured by the greater wear, which makes the internal cusps appear more circular in the present specimen. The small horns, slender zygomata, and rather small canines imply female sex. The horns are very different from those of the male *Allops*, but so also are those of the supposed female of *A. serotinus*. The evidence offered by the premolars seems to justify the reference of this skull to an advanced stage of *Allops*.

In the side view of the skull the tapering nasals suggest reference to a small species of *Brontotherium*, and this idea is at first reinforced by the general appearance of the premolars, which have large circular postero-internal cusps. But reference to *Brontotherium* is excluded by the presence of sharp external and internal cingula on the premolars, by the narrowness of the molars, and by the depth of the jaw in the region of the symphysis.

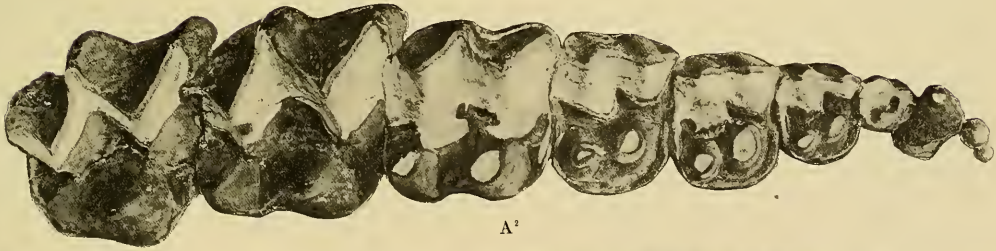
This specimen is important on account of its association with a lower jaw and with a considerable part of the skeleton. (See p. 680.)



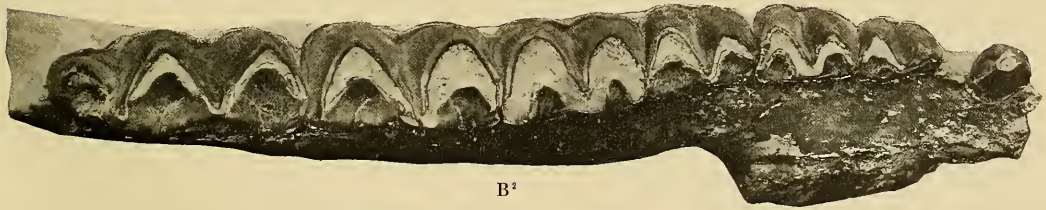
A¹



B¹



A²



B²

SKULL, JAW, AND TEETH OF ALLOPS CRASSICORNIS? SEU MARSHI

PLATE CXXIII

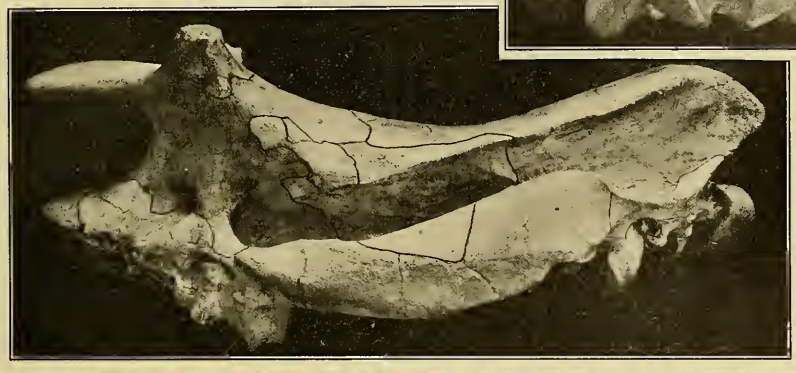
PLATE CXXIII

Type Skull of Menodus heloceras

A^1, Palatal view; A^2, top view; A^3, lateral view, left side; A^4, posterior view. One-fourth natural size. (See p. 524.)

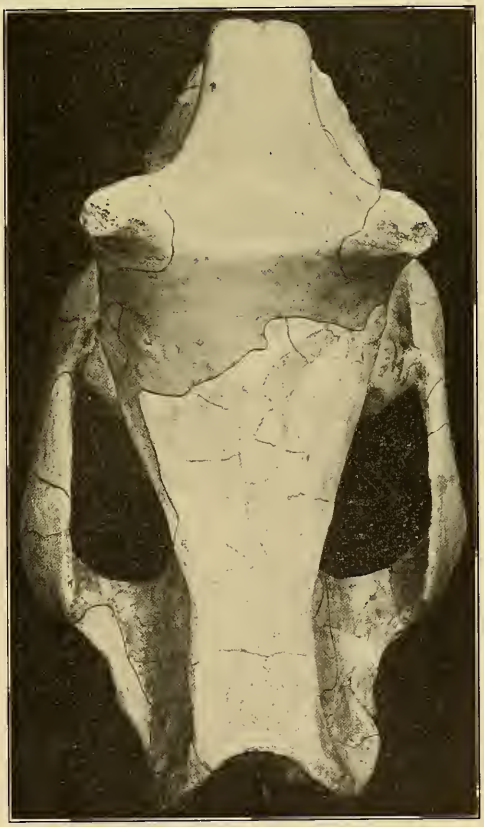
Am. Mus. 6360, type, Horsetail Creek, northeastern Colorado, Chadron formation. This very imperfect type skull exhibits well the most primitive known stage in the generic characters of *Menodus*, such as the length and slenderness, the unexpanded zygomata, and the narrow parietal crest. The horns also, although in an early phylogenetic stage, are trihedral in basal section, as in *Menodus trigonoceras*, from which the nasal region is restored. The palate is unnaturally widened by crushing. The teeth so far as preserved present nothing noteworthy. The basicranial region is elongate.

A⁴



A³

A¹



A²

TYPE SKULL OF MENODUS HELOCERAS

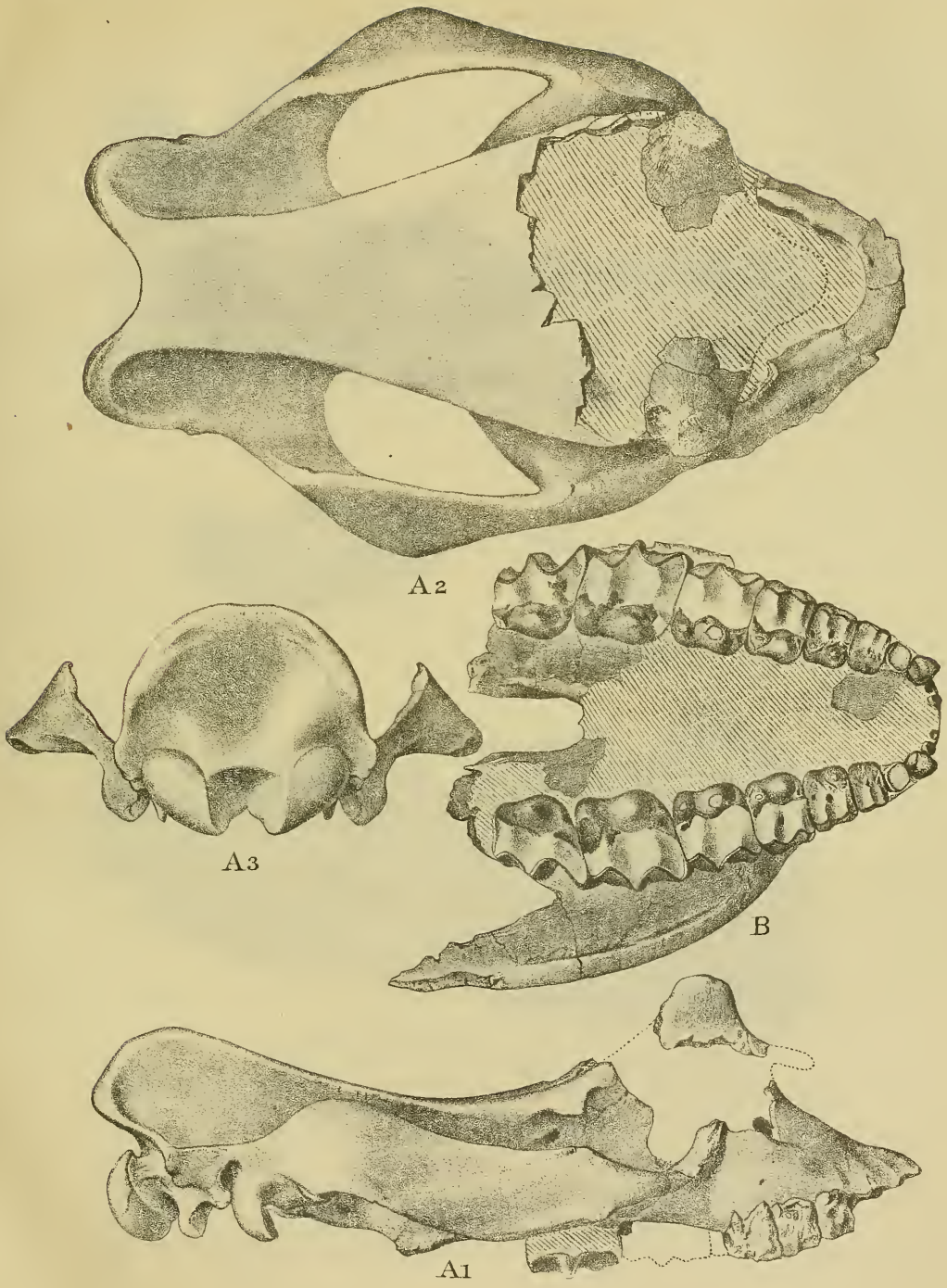
PLATE CXXIV

PLATE CXXIV

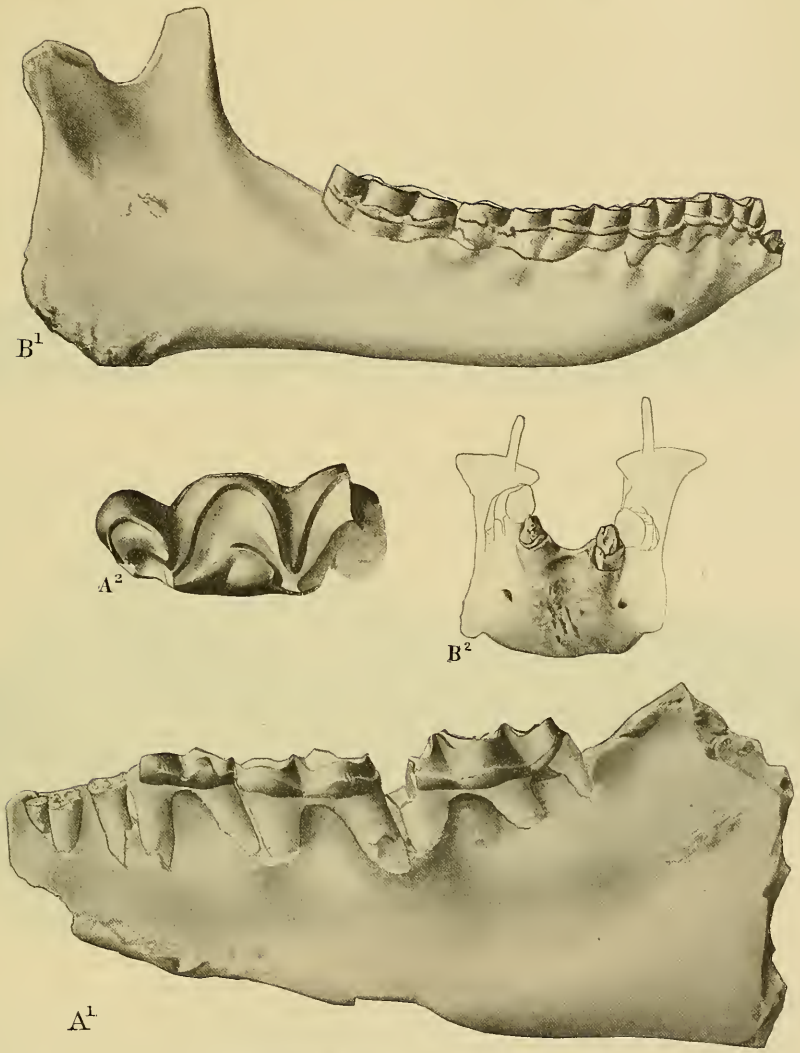
Skulls of Menodus heloceras and Brontotherium hatcheri

Plate prepared under the direction of Professor Cope. One-fourth natural size. (See p. 524, also Pl. CXXIII)

A^1, A^2, A^3, Type skull of *Menodus heloceras* (Am. Mus. 6360), Horsetail Creek, northeastern Colorado, Chadron formation.
B, *Brontotherium hatcheri* (Am. Mus. 6353), Colorado, Chadron formation. This palate was originally referred by Cope to "*Symborodon acer*," but because of the presence of incisors it is referred to *Brontotherium* by the author.



SKULLS OF MENODUS HELOCERAS, TYPE, AND BRONTOTHERIUM HATCHERI



JAWS OF MENODUS PROUTII AND MENODUS TORVUS

A[1], *Menodus proutii*, type (Nat. Mus. 113) (genotype of *Titanotherium* Leidy, see pp. 205, 527), "Mauvais Terres * * * of White River," Chadron formation. One-third natural size. Generic agreement with the genotype of *Menodus giganteus* Pomel (see p. 204) is seen in the elongate molars with sharp external cingula. The jaw fragment and teeth also agree in generic characters with the jaws Am. Mus. 1007, 1067 (see Pl. CXXXIV, A[1]), referred to *Menodus trigonoceras*. *Menodus proutii*, as represented by this jaw and by the skull Am. Mus. 9335, has the dimensions of *M. trigonoceras* and is much smaller than *M. giganteus*. A[2], *M. proutii*, imperfect third lower molar of type (Am. Mus. 113), crown view. (See A[1].) One-half natural size. The tooth shows well the heavy external cingulum of *Menodus*. B[1], B[2], *Menodus torvus*, type of *Symborodon torvus* Cope (Am. Mus. 6365), Horsetail Creek, northeastern Colorado, Chadron formation. One-fourth natural size. This is the true genotype of *Symborodon*, because Cope in his original description of *Symborodon torvus* (see p. 211) based the generic description primarily upon this jaw. It shows generic affinity with *Menodus giganteus*, and hence *Symborodon* becomes a synonym of *Menodus*. The incisors were wanting or vestigial, the premolars and molars were somewhat elongate with heavy external cingula, and the general form of the jaw recalls that of *Menodus*. The front view (B[2]) shows the edentulous incisive border. In size this type of *M. torvus* is intermediate between *M. heloceras* and *M. proutii*

A²

A¹

JAW REFERRED TO MENODUS PROUTII (TRIGONOCERAS)

One-third natural size. (See p. 524.) British Mus. 4447M. The measurements of this specimen (m_1–m_3 245 mm.) indicate close specific reference to *M. proutii*, and it might almost be selected as a neotype of that species. This jaw exhibits clearly the chief characters of *Menodus*. The cheek teeth are elongate anteriorly, with heavy external cingula; the canine is compressed and conical with heavy external cingulum; the chin is fuller than in *Brontotherium* and *Brontops*. Compare with *M. proutii* (Pl. CXXV), *M. trigonoceras*? (*giganteus*?) (Pl. CXXXIV), and *M. giganteus* (Pl. CXLI)

PLATE CXXVII

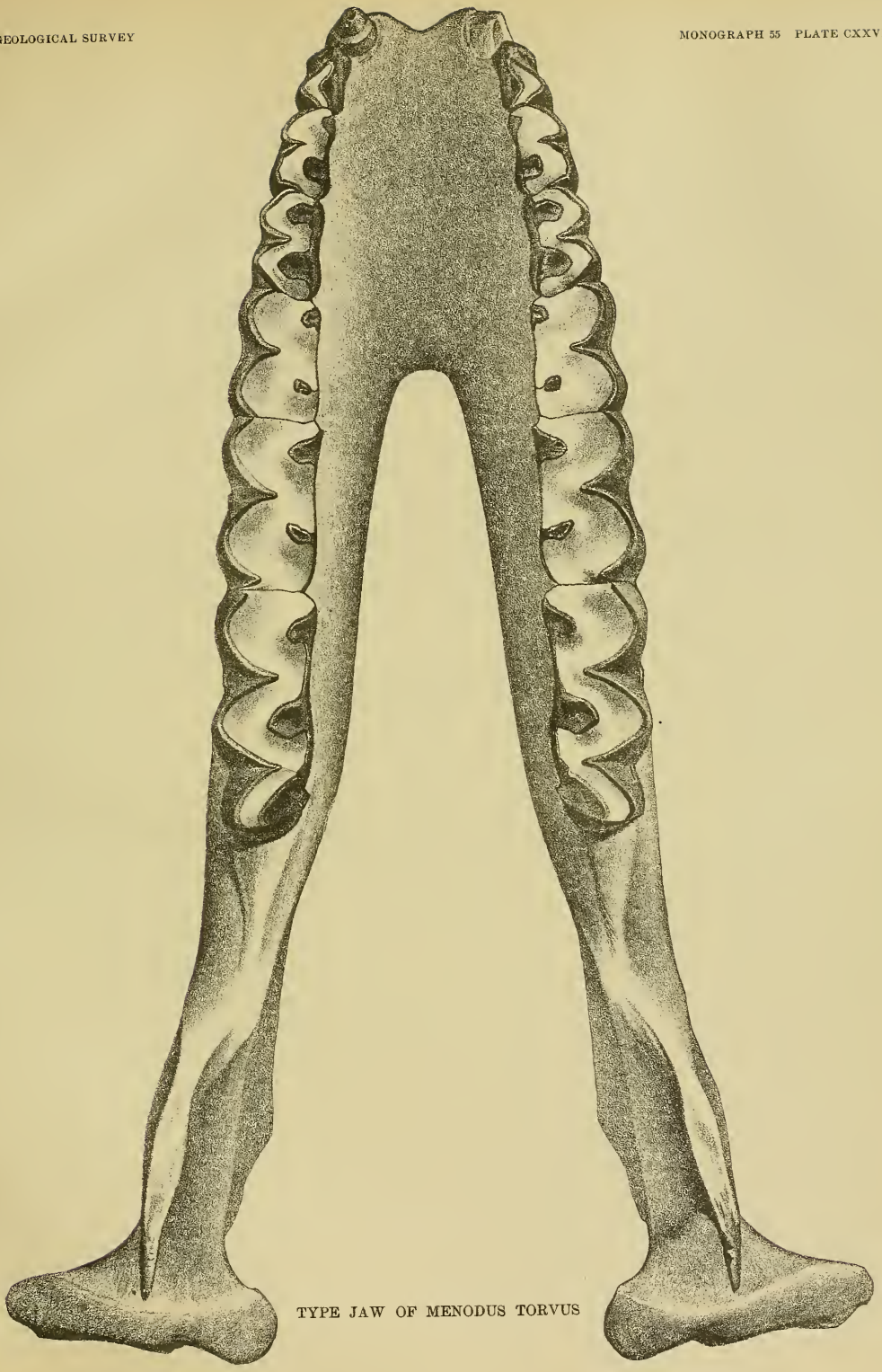
PLATE CXXVII

Type Jaw of Menodus torvus

Plate prepared under the direction of Professor Cope. One-half natural size. (See p. 210, 527, also Pls. CXXV, CLVIII, and CLIX)

Type jaw of *Symborodon torvus* Cope and genotype of *Symborodon* Cope (Am. Mus. 6365), Horsetail Creek, northeastern Colorado, Chadron formation.

Cope recognized the relationship of this animal to the species named by him "*Symborodon trigonoceras.*" This jaw is a little smaller than in the typical *M. trigonoceras.*



TYPE JAW OF MENODUS TORVUS

PLATE CXXVIII

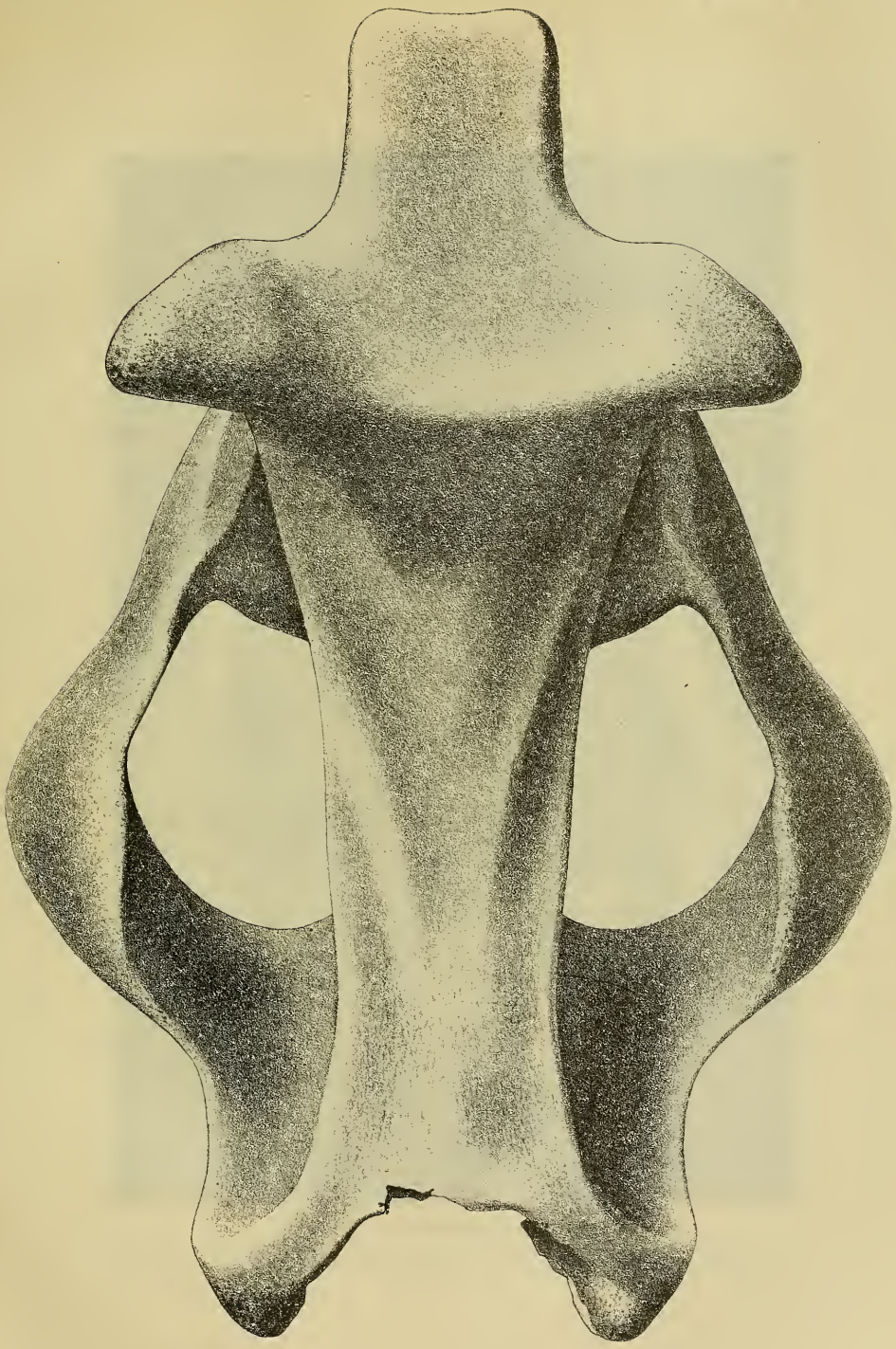
PLATE CXXVIII

Type Skull of Menodus trigonoceras

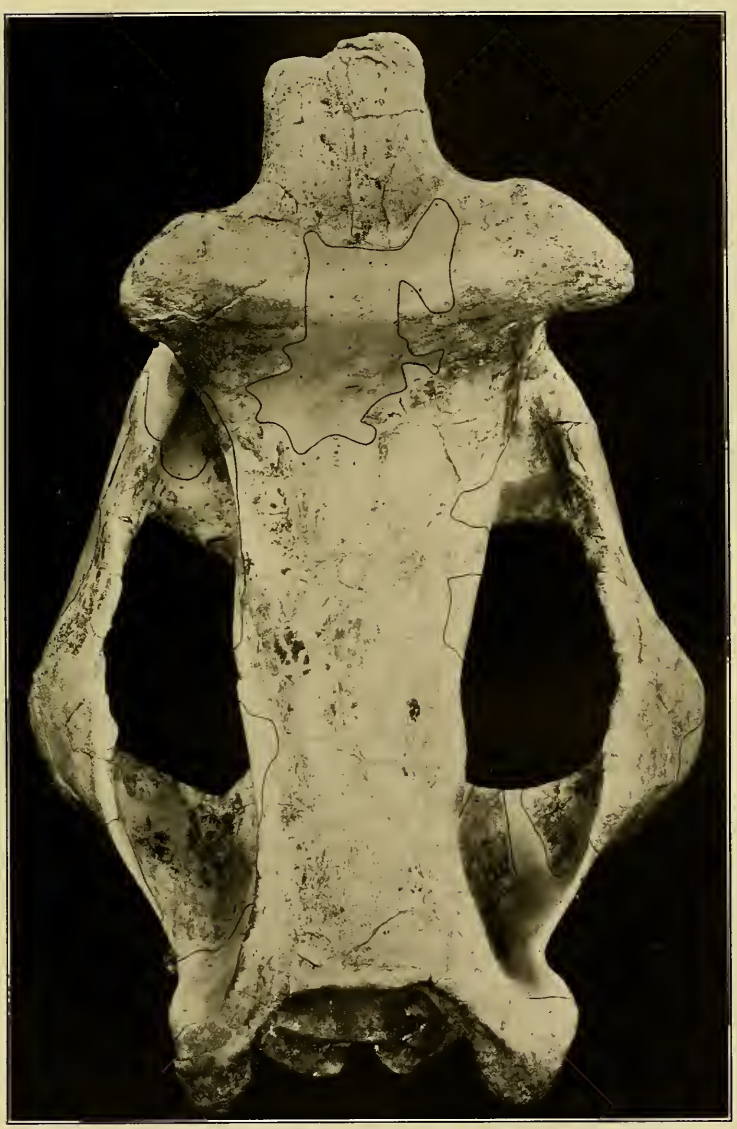
Plate prepared under the direction of Professor Cope. One-third natural size. (See p. 529, also Pl. CLVII)

Am. Mus. 6355, type, Horsetail Creek, northeastern Colorado, Chadron formation. Generic characters are displayed in the top view as follows: The skull is elongate, the zygomatic swellings are moderate (in the lithograph these swellings are too heavy and broad). The nasals are elongate and distally square. The horns are trihedral at the base, the tips pointed and recurved; the horns are directed outward and upward; the connecting crest is developed in the plane of the posterior face of the horns; the middle of the occiput is not extended behind the condyles.

A study of the table of measurements (p. 523) indicates that the lower jaw of this skull would very probably have dimensions slightly larger than those of the type jaw of *M. proutii;* it is quite possible that *M. trigonoceras* may prove to be specifically identical with *M. proutii* and therefore a synonym.



TYPE SKULL OF MENODUS TRIGONOCERAS



TYPE SKULL OF MENODUS TRIGONOCERAS

Am. Mus. 6355, Horsetail Creek, northeastern Colorado, Chadron formation. One-fourth natural size. This view shows the restored parts in outline. (Compare *Menodus giganteus*, Pl. CXL)

PLATE CXXX

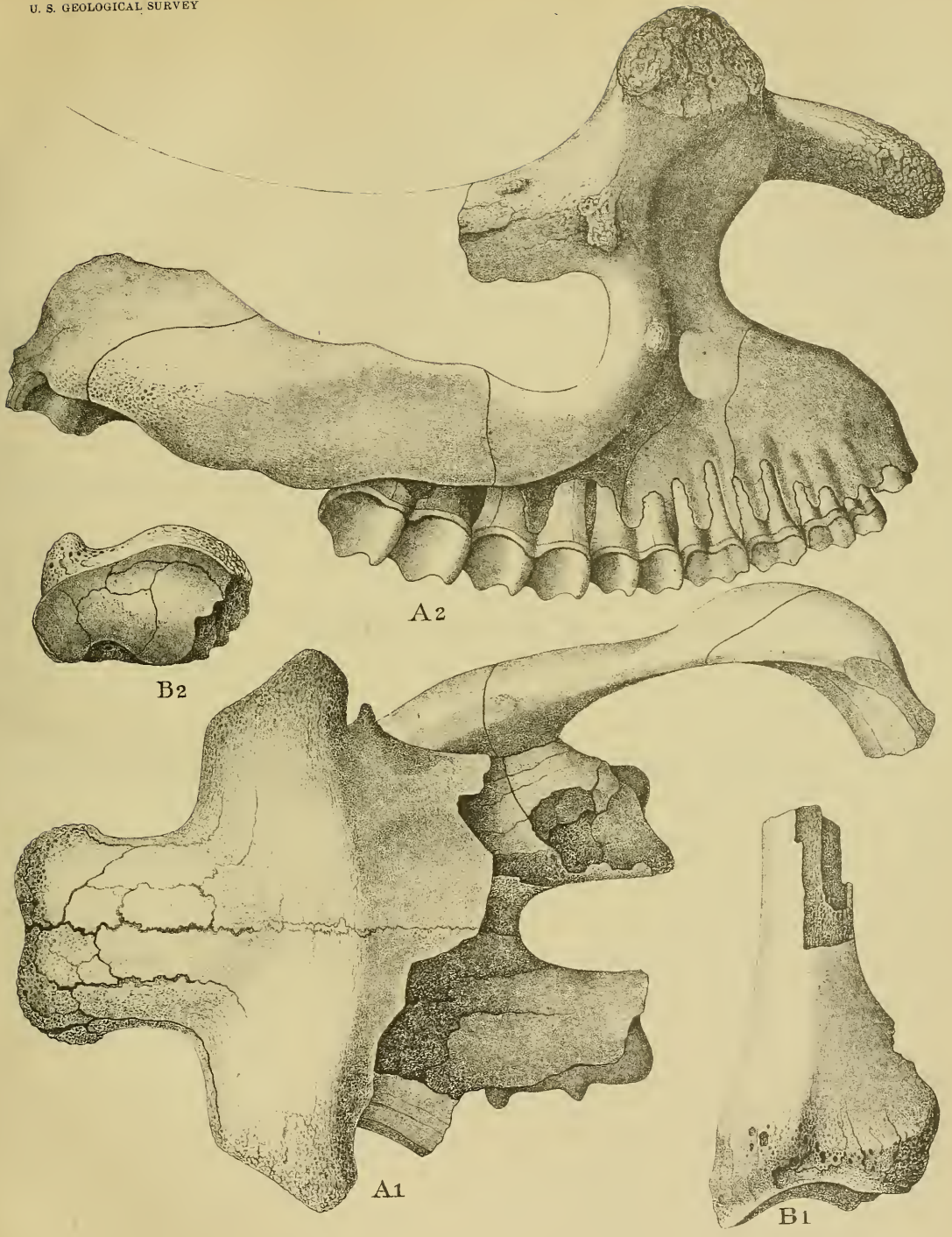
PLATE CXXX

Skull of Menodus trigonoceras (Cotype) and a Radius Doubtfully Referred

Plate prepared under the direction of Professor Cope. One-third natural size. (See pp. 214, 529)

A_1, A_2, Am. Mus. 6356, cotype, Horsetail Creek, northeastern Colorado, Chadron formation. This skull shows the elongate, distally expanded nasals and the trihedral, outward-directed horns of *Menodus*.

B_1, B_2, Left radius, front and distal views of the lower portion. The reference of this fragment to *M. trigonoceras* is doubtful.



SKULL OF MENODUS TRIGONOCERAS, COTYPE, AND A RADIUS DOUBTFULLY REFERRED

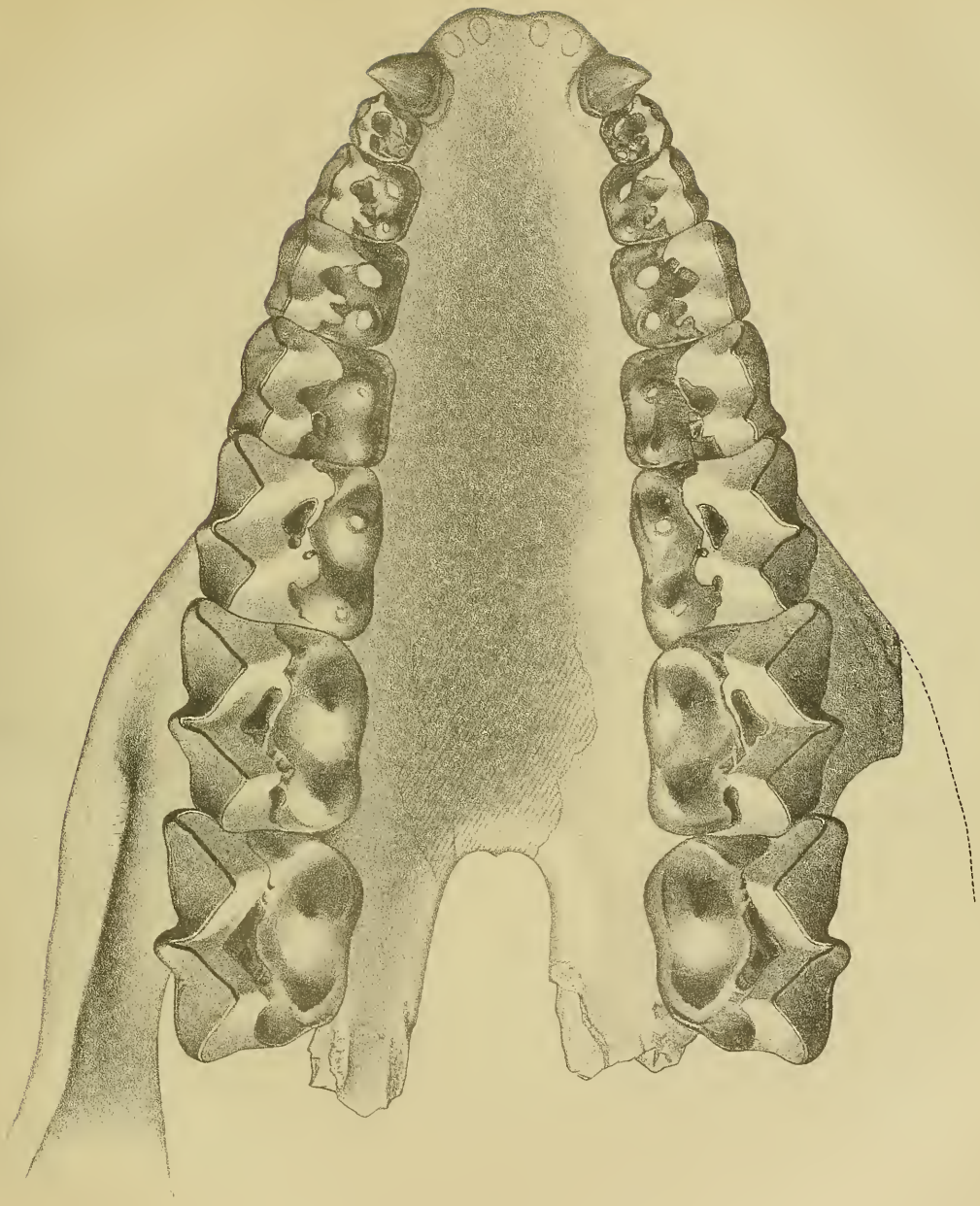
PLATE CXXXI

PLATE CXXXI

Palate of Menodus trigonoceras

Plate prepared under the direction of Professor Cope. One-half natural size. (See p. 529)

Am. Mus. 6356, Horsetail Creek, northeastern Colorado, Chadron formation. Upper teeth of cotype skull. The teeth are more accurately figured in Plate CXXXII, B, but this lithograph shows well enough the anteroposteriorly elongate molars and the progressive premolar cusps of *Menodus*. The external cingula should have been more clearly defined. The incisor alveoli are represented too large, as the specimen shows that the roots of the incisors were small, as in *Menodus*.



PALATE OF MENODUS TRIGONOCERAS

PLATE CXXXII

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PLATE CXXXII

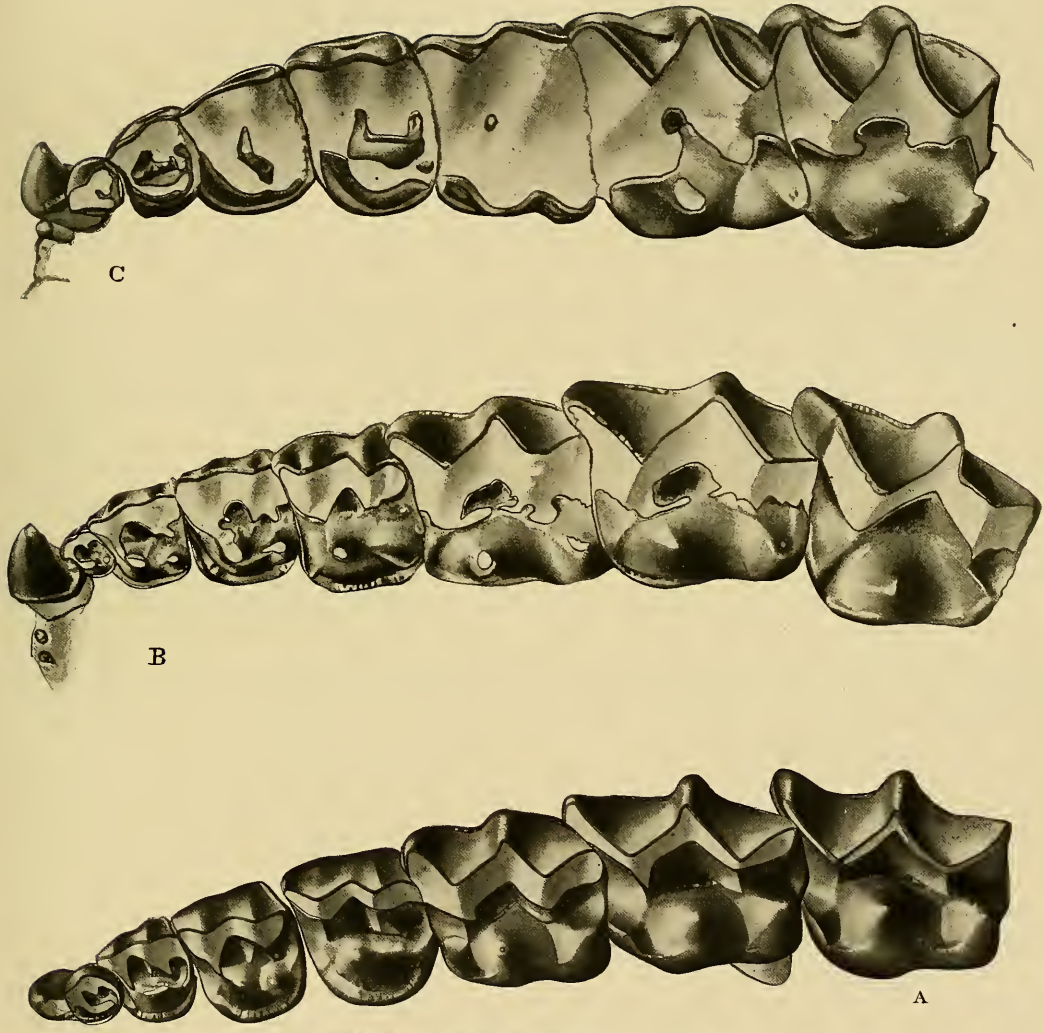
Upper Molar Series of Menodus and Allops

One-half natural size. (See p. 523)

A, Molars referred to *Menodus torvus?*, Carnegie Mus. 558 or 3068. This specimen represents a stage between the more primitive *M. heloceras* and the more advanced *M. proutii* (*trigonoceras*). It is considerably larger than *M. heloceras;* it is smaller and much more primitive than *M. proutii* (*trigonoceras*), in the form both of its premolars, which have small postero-internal cusps and rounded internal borders, and of its molars, which are narrower. The dimensions of the teeth approach those which we might expect to find in the upper teeth of *M. torvus*, a form hitherto known only from the lower jaw.

B, Upper teeth of *Menodus trigonoceras*, cotype (Am. Mus. 6356), Horsetail Creek, northeastern Colorado, Chadron formation. The drawing shows the alveoli for the vestigial incisors, the conical cingulate canine, the sharp cingula of the premolars and molars, the well-developed postero-internal cusps of the premolars, joined by narrow ridges to the antero-internal cusps, and the relatively elongate molars—all characteristic of *Menodus*.

C, Molars referred to *Allops serotinus* (Am. Mus. 520), Cheyenne River, S. Dak., Chadron formation. The teeth of *Allops* differ from those of *Menodus* as follows: One or two upper incisors persist on each side; the canine is flattened anteroposteriorly, the premolars and molars are wider transversely, the postero-internal cusps of the premolars in *A. serotinus* are less distinct than in *Menodus*. In all these characters, except the flattening of the canine, *Allops* resembles *Brontops*.



UPPER MOLAR SERIES OF MENODUS AND ALLOPS

PLATE CXXXIII

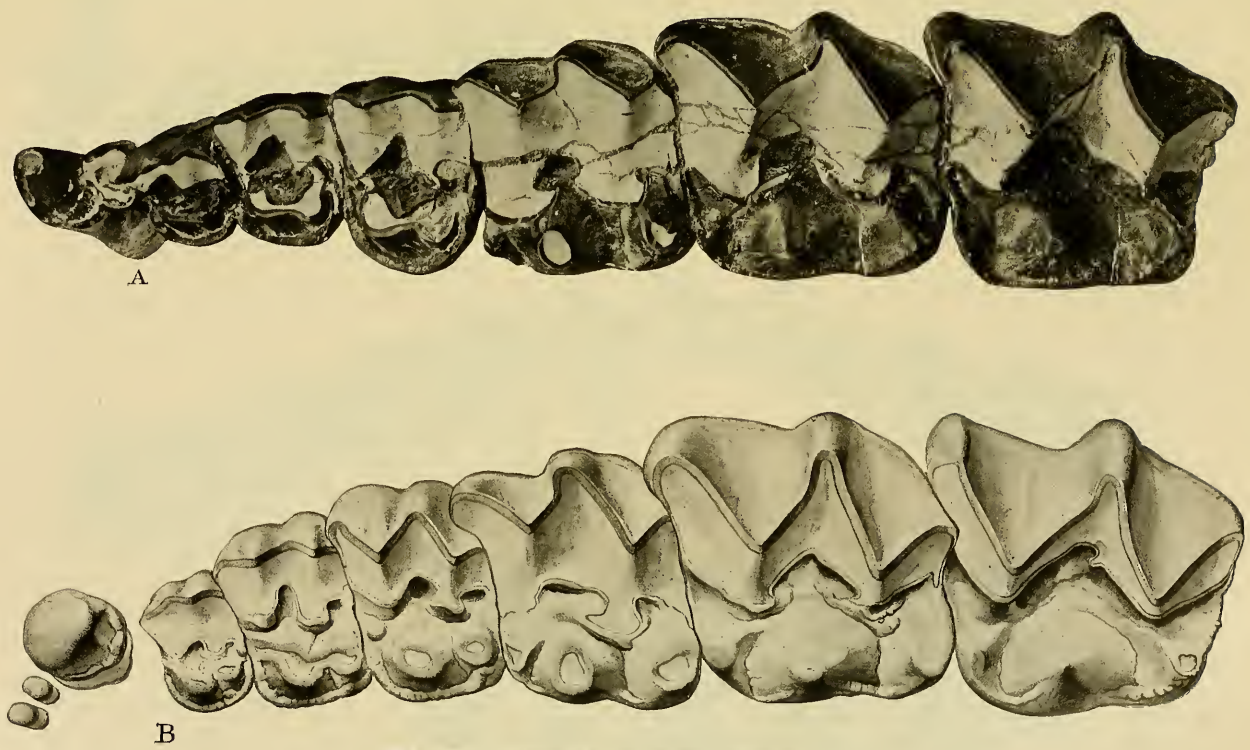
PLATE CXXXIII

Upper Teeth of Menodus and Brontotherium

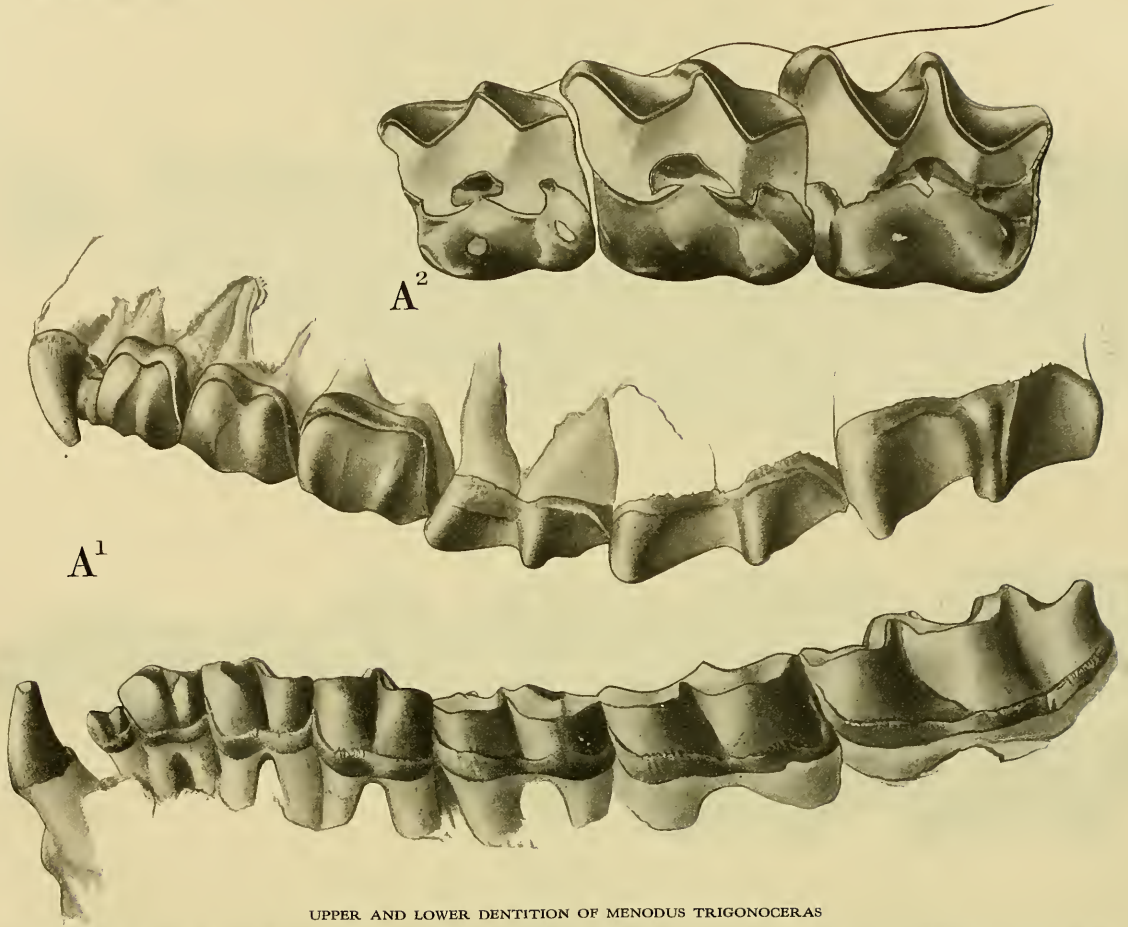
One-half natural size. (See pp. 523, 554)

A, *Menodus giganteus*, neotype (Am. Mus. 505), South Dakota, probably Cheyenne River, Chadron formation.
B, *Brontotherium gigas* (Am. Mus. 492), Cheyenne River Badlands, S. Dak., Chadron formation.
The chief contrasts shown in these figures are as follows:

	Menodus (A)	Brontotherium (B)
Upper incisors	Vestigial or none	Two incisors, large and typically flat topped.
Canines	Long, conic	Short, recurved, swelling, with massive posterior cingulum.
Premolars	Transversely narrower, less molariform, with postero-internal cusps connected with antero-internal cusps by a long, slender bridge.	Very broad, more molariform, postero-internal cusps very large, subcircular, and barely if at all connected with antero-internal cusps.
Internal border of p^4	Rounded	Subquadrate.
External V's of fourth premolar	Barely suggested	Well defined.
External cingulum of premolars	Very sharp	Obsolete.
Internal cingulum of premolars	Sharp	Massive or partly confluent with base of crown.
Protostyles of premolars and molars	Feeble or absent	Very large.
Hypocones of m^1, m^2	Less protuberant internally	More protuberant.
Proportions of molars	More elongate anteroposteriorly	Wider.
External cingulum of molars	Sharply defined	Obsolete.
Internal cingulum of molars	Delicate, more or less continuous	Discontinuous—that is, lacking opposite protocones.



UPPER TEETH OF MENODUS AND BRONTOTHERIUM



UPPER AND LOWER DENTITION OF MENODUS TRIGONOCERAS

One-half natural size. (See pp. 523, 528.) Female of *Menodus trigonoceras*? (Am. Mus. 1067), Hat Creek Badlands, Nebr., Chadron formation. A^1, External view of the upper and lower teeth; A^2, crown view of the upper molars. This supposed female skull (see Pl. CXXXV) has slender recurved canines. The cheek teeth are heavily cingulate and of elongate proportions. The first premolars, both upper and lower, are small. In m^3 the hypocone is surrounded by the cingulum. In the dimensions of the teeth as well as of the skull this specimen is distinctly smaller than a supposed female of *M. giganteus* (Am. Mus. 506); but it is a little larger than *M. trigonoceras* and *M. proutii*

PLATE CXXXV

PLATE CXXXV

Skulls of Menodus trigonoceras? and Menodus giganteus

One-fourth natural size. (See pp. 523, 528, 531)

A, Skull of female *Menodus trigonoceras?* (Am. Mus. 1067), Hat Creek Badlands, Nebr., Chadron formation. Front view of distorted skull with associated lower jaw. This specimen is smaller than the supposed female of *M. giganteus* (B), but it is a little larger than the cotype of *M. trigonoceras.* It may be a female of *M. varians,* which it somewhat resembles in the right horn. The incisive borders were apparently edentulous. The slender canines are cingulate. The thick horns are trihedral in basal section, the left horn badly distorted. The nasals are wide distally, with two small processes on each side of a median notch. These processes with the whole rugose end of the nasals probably served for the attachment of a powerful levator labii superioris muscle. The buccal swellings of the zygomata are small.

B, Skull of female of *M. giganteus* (Am. Mus. 506), Big Badlands, Cheyenne River, S. Dak., Chadron formation. This skull illustrates well the effect of lateral crushing. Slender proportions are shown by the horns, canines, and zygomata. In dental measurements this skull is somewhat inferior to those in the males of *M. ingens.*

A B

SKULLS OF MENODUS TRIGONOCERAS? AND MENODUS GIGANTEUS

PLATE CXXXVI

PLATE CXXXVI

Skull of Menodus giganteus

One-fourth natural size. (See pp. 523, 531, also Pl. CXXXV)

Am. Mus. 506, female, Big Badlands, Cheyenne River, S. Dak., Chadron formation. Crushed skull and associated lower jaw. The horns are much smaller than in the males of this species. The buccal swellings of the zygomata were very slight. The dental characters noted in Plate CXXIV are also shown here. The contour of the lower jaw, although somewhat distorted, conforms in general with that of *Menodus giganteus*. (See Pl. CXXXIX.)

SKULL OF MENODUS GIGANTEUS

PLATE CXXXVII

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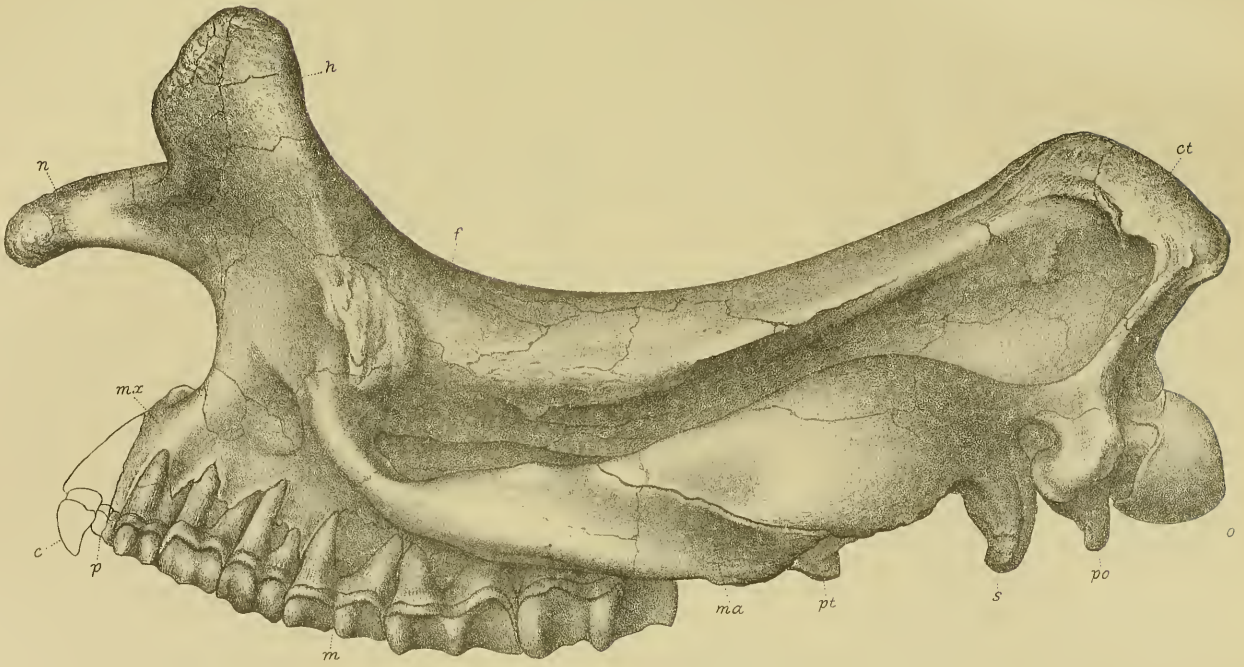
PLATE CXXXVII

Skull of Menodus giganteus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. Side view. (See pp. 523, 532)

Type of "*Brontotherium ingens*" Marsh (Yale Mus. 12010), Colorado, Chadron formation. This fine skull, which Marsh erroneously referred to *Brontotherium*, possesses all the distinctive characters of *Menodus*, among which may be noted the following: Skull dolichocephalic, with slight zygomatic expansion and narrow parietal vertex; horns divergent, trihedral in basal section, connecting crest at back of horns; nasals elongate, wide distally; cheek teeth with sharp external cingula.



SKULL OF MENODUS GIGANTEUS

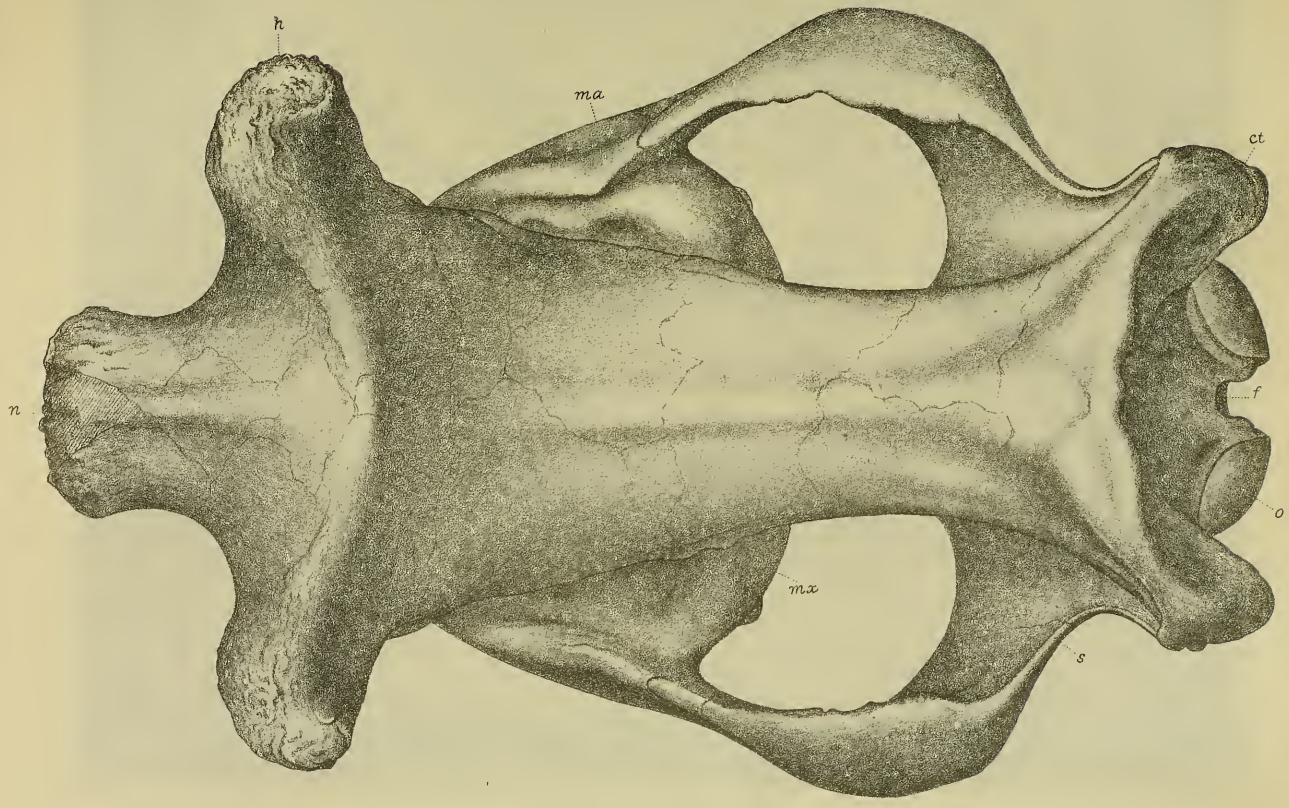
PLATE CXXXVIII

PLATE CXXXVIII

Skull of Menodus giganteus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. Top view. (See pp. 523, 532 and Pl. CXXXVII)

2



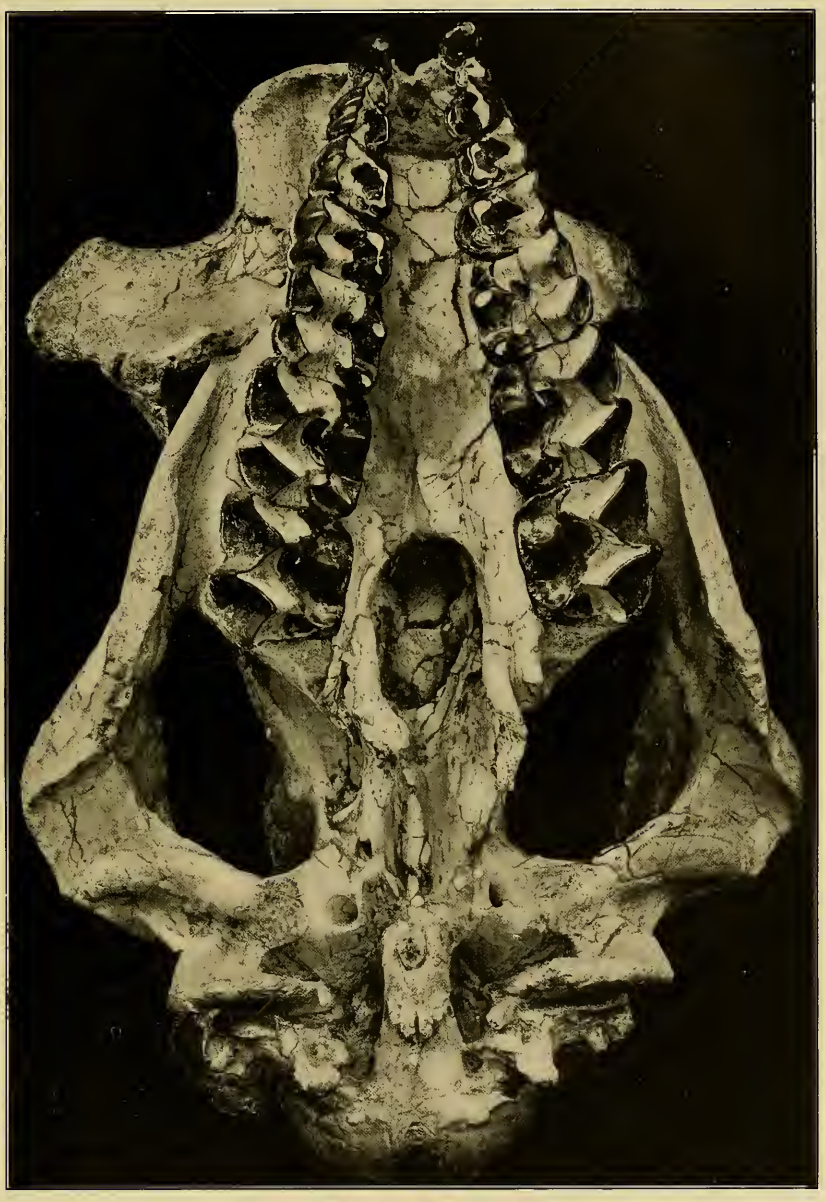
SKULL OF MENODUS GIGANTEUS

SKULL OF MENODUS GIGANTEUS

One-fifth natural size. (See pp. 523, 532, also Pl. CXL.) Field Mus. P 5927, male, Phinney Springs, S. Dak., Chadron ormation, uppermost level. This superb skull with associated lower jaw shows the final stage of the *Menodus* phylum. It is considerably larger than the type of *M. ingens* in basilar length and in dental measurements. (See p. 523.) It is very dolichocephalic, with long nasals and large horns, conical cingulate canines, and elongate grinding teeth

SKULL OF MENODUS GIGANTEUS

One-fourth natural size. (See pp. 523, 532, also Pl. CXXXIX.) Field Mus. P 5927, male, Phinney Springs, S. Dak., Chadron formation, uppermost level. The front view shows the great length and tapering character of the horns, the functionally edentulous incisive borders, the great width of the nasals, and the moderate expansion of the zygomata



SKULL OF MENODUS GIGANTEUS

One-fourth natural size. (See p. 532.) Am. Mus. 505, male, Big Badlands, S. Dak., probably Cheyenne River, Chadron formation. This skull exhibits the dental and cranial characters of *Menodus giganteus* as described above. (See Pls. CXXXIII, CXXXVII, CXXXVIII, and CXXXIX.) The horns show well the pointed tips and flattened external base. The basicranial region shows the alisphenoid canal, the foramen ovale, the paired and median protuberances for the recti capitis antici muscles, the periotic bone, the proximal end of the stylohyoid, and the condylar foramen

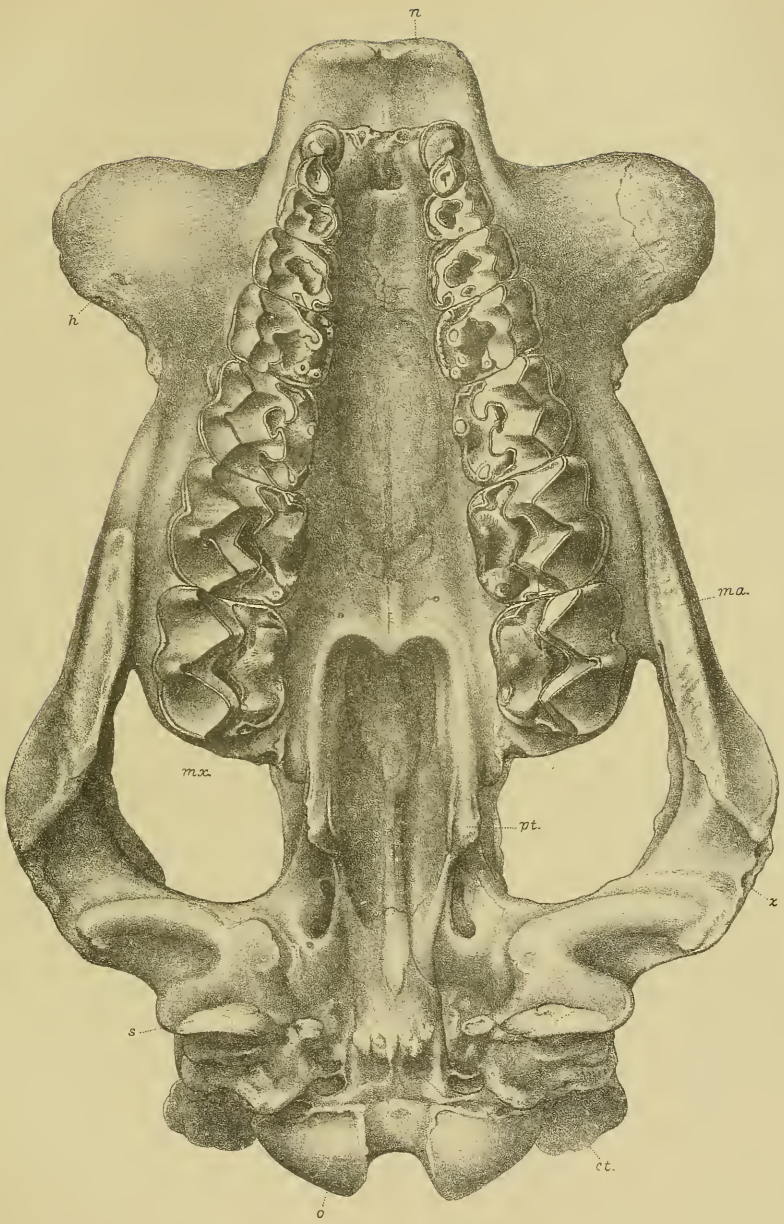
PLATE CXLII

PLATE CXLII

Type Skull of Menodus varians

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 536)

Menodus (*Menops*) *varians* Marsh, type (Yale Mus. 12060), South Dakota, Chadron formation. This skull is referred to *Menodus* on the following grounds: It is dolichocephalic, with little zygomatic expansion; the incisors are reduced or vestigial; the canines are conical and cingulate; the cheek teeth are elongate anteroposteriorly, and the premolars and molars have the chief characters described above (Pl. CXXXIII); the nasals are long and distally broad, and the horns are trihedral at the base; the dental and other measurements in general agree with those of *Menodus giganteus*. Noteworthy features of the dentition are the presence of an accessory cusp behind the postero-internal cusp of p^4 (a rare or unique character); the great size and depth of the medifossettes of the premolars; the advanced development of the protostyles of the molars; the quadrate character of m^3, which has the well-developed hypocone surrounded posteriorly by a broad cingulum. These characters, together with the thickened tips of the horns, the greater width of the skull, and the widened base of the nasals, appear to indicate a mutation or species distinct from the typical *M. giganteus* (*"ingens"*). From *Allops crassicornis* (see Pl. CXX) the present form is distinguished by its more pronounced dolichocephalic characters, especially in the dentition.



TYPE SKULL OF MENODUS VARIANS

PLATE CXLIII

PLATE CXLIII

Type Skull of Megacerops copei

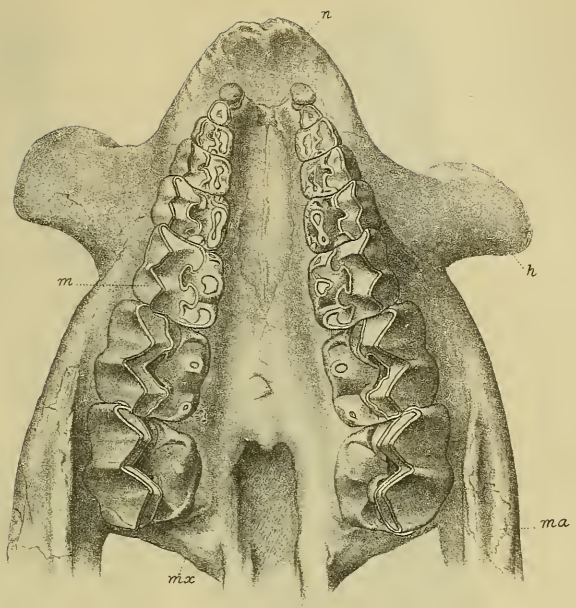
Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See pp. 543, 548, also Pl. CXLIV)

Skull V^1, type (Nat. Mus. 4711), Big Badlands, Indian Draw, S. Dak., Chadron formation, level upper C (Hatcher). A_1, Side view; A_2, palate.

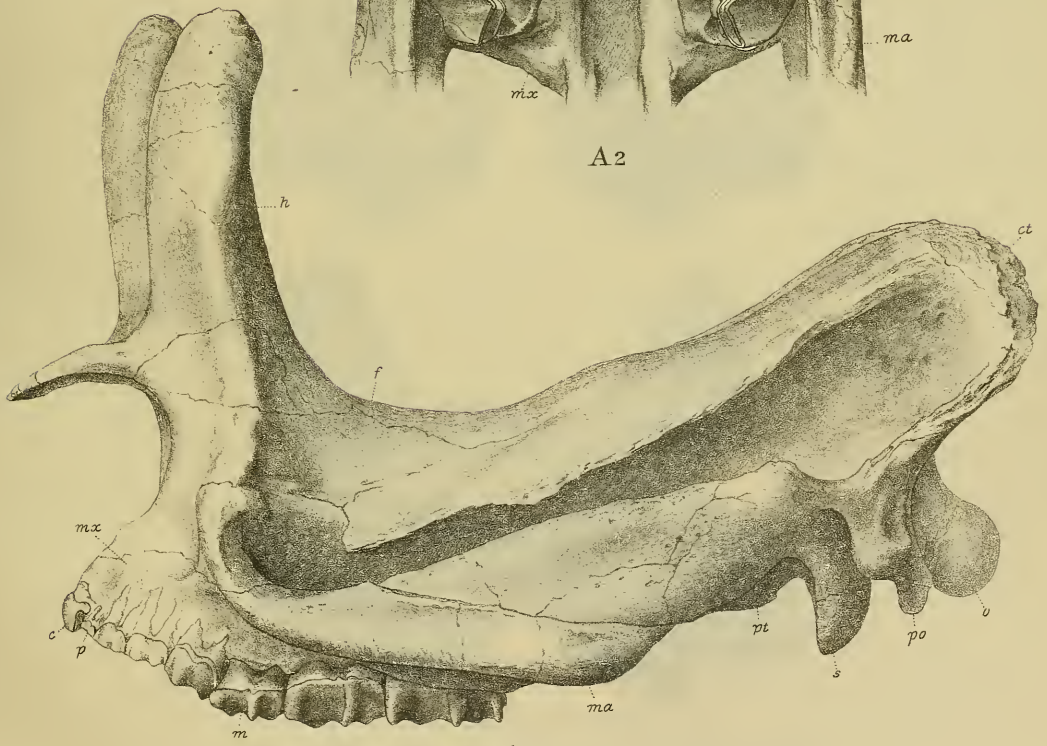
The vertical position of the horns in this figure is largely due to crushing. A more accurate representation of the teeth is given in Plate CXLV.

This skull was referred by Marsh to *Menodus* (=*Diconodon*) *montanus* but differs generically from the type in the nasals, premolars, and molars.

Characteristic *Megacerops* features observed in this skull are the extremely short face, upturned premolar series, small and closely approximated canines, horns of subcylindrical basal section without connecting crest. Affinity with *Brontotherium* is seen in the general contour of the skull, midparietal convexity, expanded zygomata, decurved nasals, advanced submolariform premolars, and short, bulbous canines.

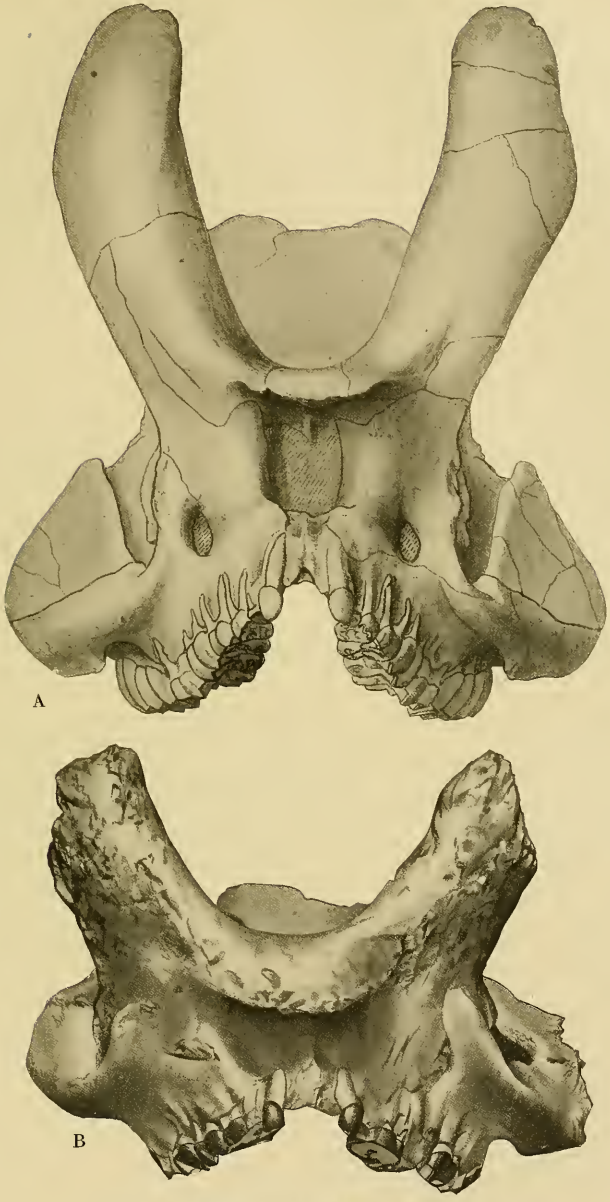


A2



A1

TYPE SKULL OF MEGACEROPS COPEI



SKULLS OF MEGACEROPS COPEI AND M. BUCCO

One-fourth natural size. (See pp. 543, 544, 548, also Pls. CXLIII and CXLV.) A, *Megacerops copei*, skull V^1, type (Nat. Mus. 4711), Indian Draw, Big Badlands, S. Dak., Chadron formation, level upper C (Hatcher). In this front view lateral crushing has emphasized the erect position of the horns. The close appression of the zygomata to the brain case is also due to crushing. This skull differs from *M. acer*, especially in the horns. Figure prepared under the direction of Professor Marsh. B, Female skull referred to *Megacerops bucco*, skull O^1 (Nat. Mus. 4705), South Dakota, *Titanotherium* zone, upper levels of middle part (Hatcher). Figure prepared under the direction of the author. Vertical crushing has diminished the vertical and increased the transverse diameters of this specimen. Its resemblances to the male of *M. bucco* as well as to the female of *M. acer* may be noted in Plates CLV and CL, B

PLATE CXLV

PLATE CXLV

Skulls of Megacerops copei and M. bucco

One-fourth natural size. (See pp. 543, 544, 548, also Pls. CXLIII and CXLIV)

A, *Megacerops copei*, skull V^1, type (Nat. Mus. 4711), Indian Draw, Big Badlands, S. Dak., Chadron formation, level upper C (Hatcher). The skull is crushed laterally, thus concealing its brachycephaly. The premolars are in an advanced stage; witness the large round postero-internal cusps and submolariform appearance of p^4. The molars are very large, with large protostyles and jutting hypocones. The canines are short and stumpy.

B, Female skull referred to *Megacerops bucco*, skull O^1 (Nat. Mus. 4705), South Dakota, *Titanotherium* zone, upper levels of middle part (Hatcher). A very old supposed female. P^4 very progressive, with a large mesostyle; premolars with reduced internal cingula; canines very small. Skull very brachycephalic, zygomata widely expanded (unusual in females).

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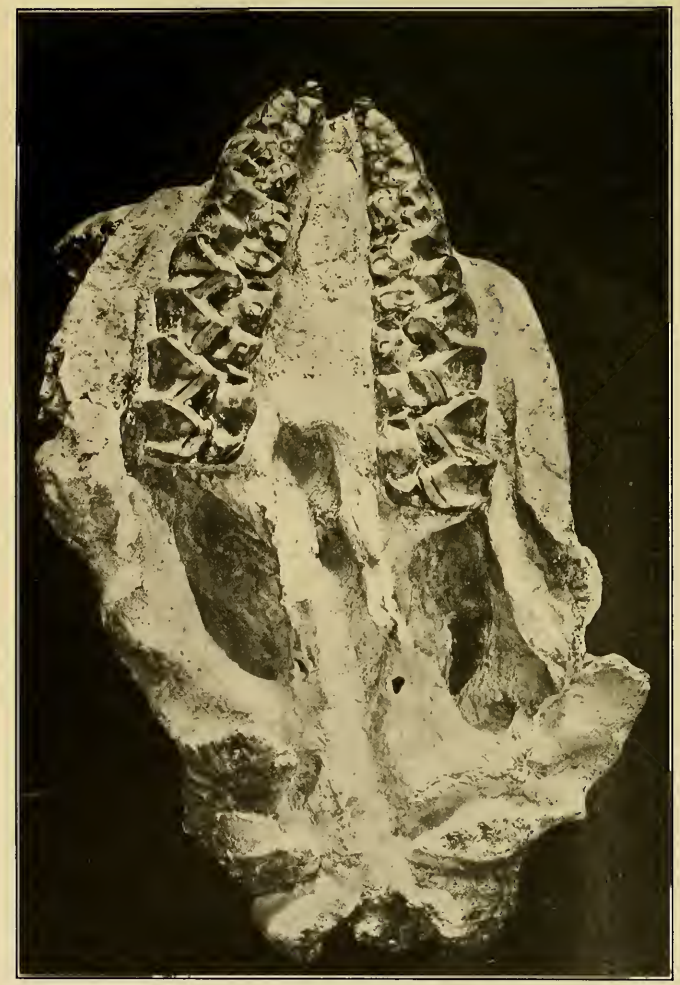
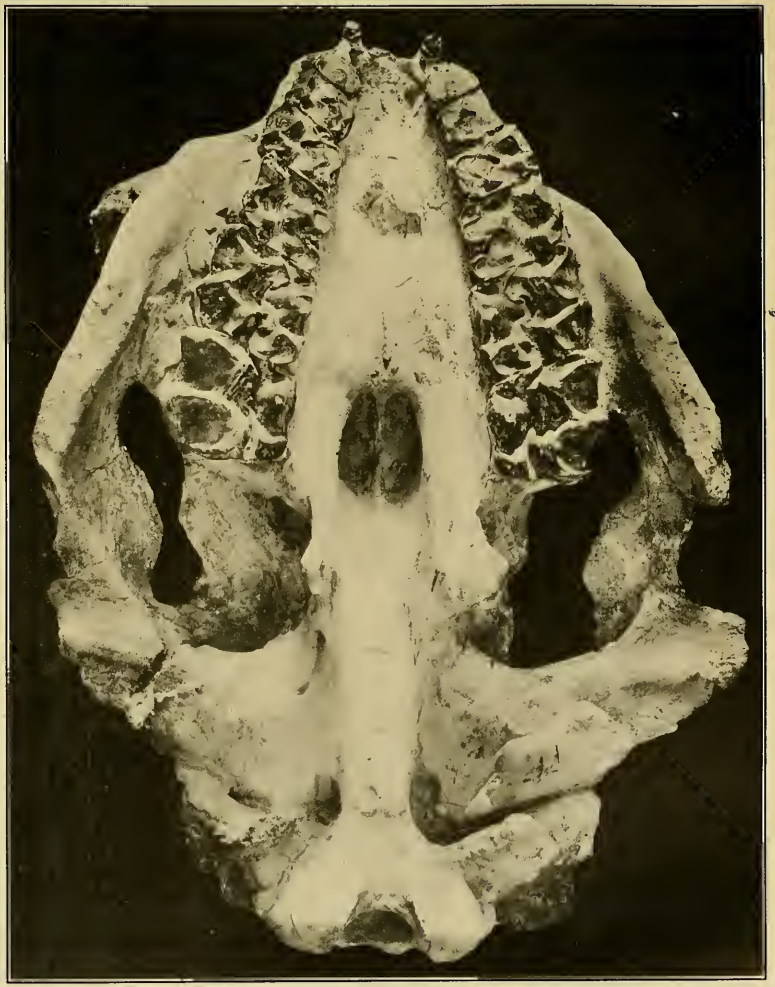


A



B

SKULLS OF MEGACEROPS COPEI AND M. BUCCO

PLATE CXLVI

PLATE CXLVI

Skulls of Megacerops acer

Side view. One-fourth natural size. (See p. 545)

A, Type (Am. Mus. 6348), Horsetail Creek, northeastern Colorado, Chadron formation. A more perfect skull of this species is shown in Figure 452, p. 548. Horns elongate, subcylindrical in basal section, with low connecting crest. Affinity with *Brontotherium* seen in general configuration of nasals, horns, and cranium.

B, Referred female skull (Am. Mus. 6350; type of *Symborodon altirostris* Cope), Horsetail Creek, northeastern Colorado, Chadron formation. Regarded by Osborn as a female of *M. acer*, but the specific reference is uncertain. The basal section of the horns and the general configuration of the skull are similar to *M. acer*, but the nasals are shorter; the horns are also short and without connecting crest. The front view (Pl. CL, B) shows well the high position of the nasals (*"altirostris"*), the alveoli for two small incisors, the large, rounded opening of the infraorbital canal. Affinity with the supposed female of *M. bucco* (figured in Pl. CXLV) is indicated, especially in the top view (Pl. CXLVIII) and in the palate (Pl. CL; compare Pl. CLII).

B

A

SKULLS OF MEGACEROPS ACER

PLATE CXLVII

PLATE CXLVII

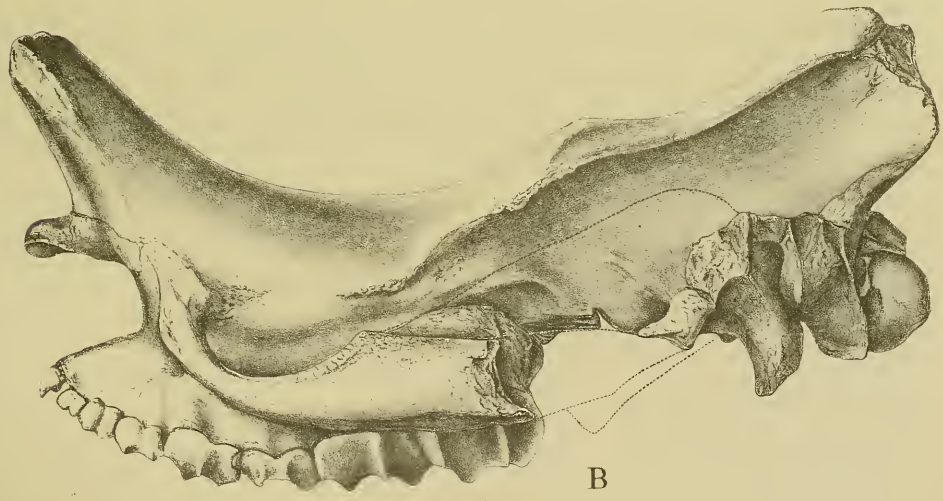
Skulls of Megacerops acer

Plate prepared under the direction of Professor Cope. Side view. One-fourth natural size. (See p. 545, also Pl. CXLVI)

A, Type (Am. Mus. 6348), Horsetail Creek, northeastern Colorado, Chadron formation.

B, Female skull referred to *M. acer?* (Am. Mus. 6350), Horsetail Creek, northeastern Colorado, Chadron formation. This is Cope's type of *Symborodon altirostris*. The canine tooth, which has since been lost, was more robust than in the supposed female figured in Plate CXLV.

A



B

SKULLS OF MEGACEROPS ACER

PLATE CXLVIII

PLATE CXLVIII

Skulls of Megacerops acer

Top view. One-fourth natural size. (See p. 545, also Pl. CXLVI)

A, Referred female skull (Am. Mus. 6350; type of *Symborodon altirostris* Cope), Horsetail Creek, northeastern Colorado, Chadron formation. (Compare with supposed *M. bucco* female, Pl. CLVI.)

B, Type (Am. Mus. 6348), Horsetail Creek, northeastern Colorado, Chadron formation. The top of the skull is long and comparatively narrow, as in males of *Brontotherium*.

A

B

SKULLS OF MEGACEROPS ACER

PLATE CXLIX

PLATE CXLIX

Skulls of Megacerops acer

Plate prepared under the direction of Professor Cope. Top view. One-fourth natural size. (See p. 545, also Pl. CXLVII)

A, Female skull referred to *M. acer?* (Am. Mus. 6350; type of *Symborodon altirostris* Cope), Horsetail Creek, northeastern Colorado, Chadron formation. This figure is not as accurate as the photographic figures in Plate CXLVII. Affinity with *M. bucco* is indicated.

B, Type (Am. Mus. 6348), Horsetail Creek. northeastern Colorado.

A B

SKULLS OF MEGACEROPS ACER

A

B

SKULLS OF MEGACEROPS ACER

Front view. One-sixth natural size. (See p. 545.) A, Type (Am. Mus. 6348), Horsetail Creek, northeastern Colorado, Chadron formation. Horns elongate, subcylindrical in basal section, with low connecting crest. Affinity with *Brontotherium* seen in general configuration of nasals, horns, and cranium. B, Female skull referred to *M. acer?* (Am. Mus. 6350; type of *Symborodon altirostris* Cope), Horsetail Creek, northeastern Colorado, Chadron formation. The basal section of the horns and the general configuration of the skull are similar to *M. acer*, but the nasals are shorter; the horns are also short and without connecting crest. This view shows well the high position of the nasals ("*altirostris*"), the alveoli for two small incisors, and the large, rounded opening of the infraorbital canal. Affinity with the supposed female of *M. bucco* (Pl. CXLV) is indicated, especially in the top view (Pl. CXLVII) and in the palate (Pl. CXLIX). (Compare Pl. CLI)

PLATE CLI

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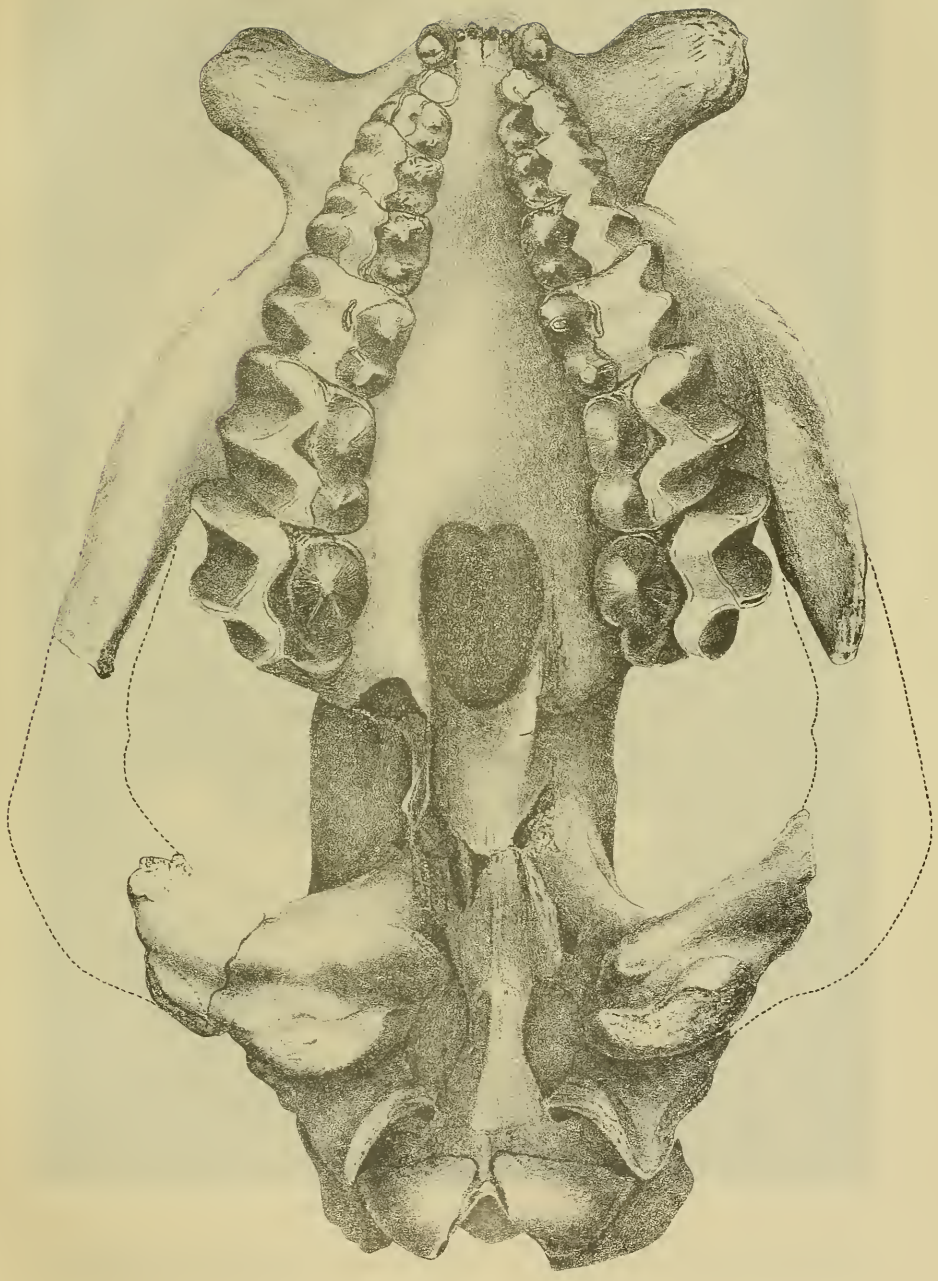
PLATE CLI

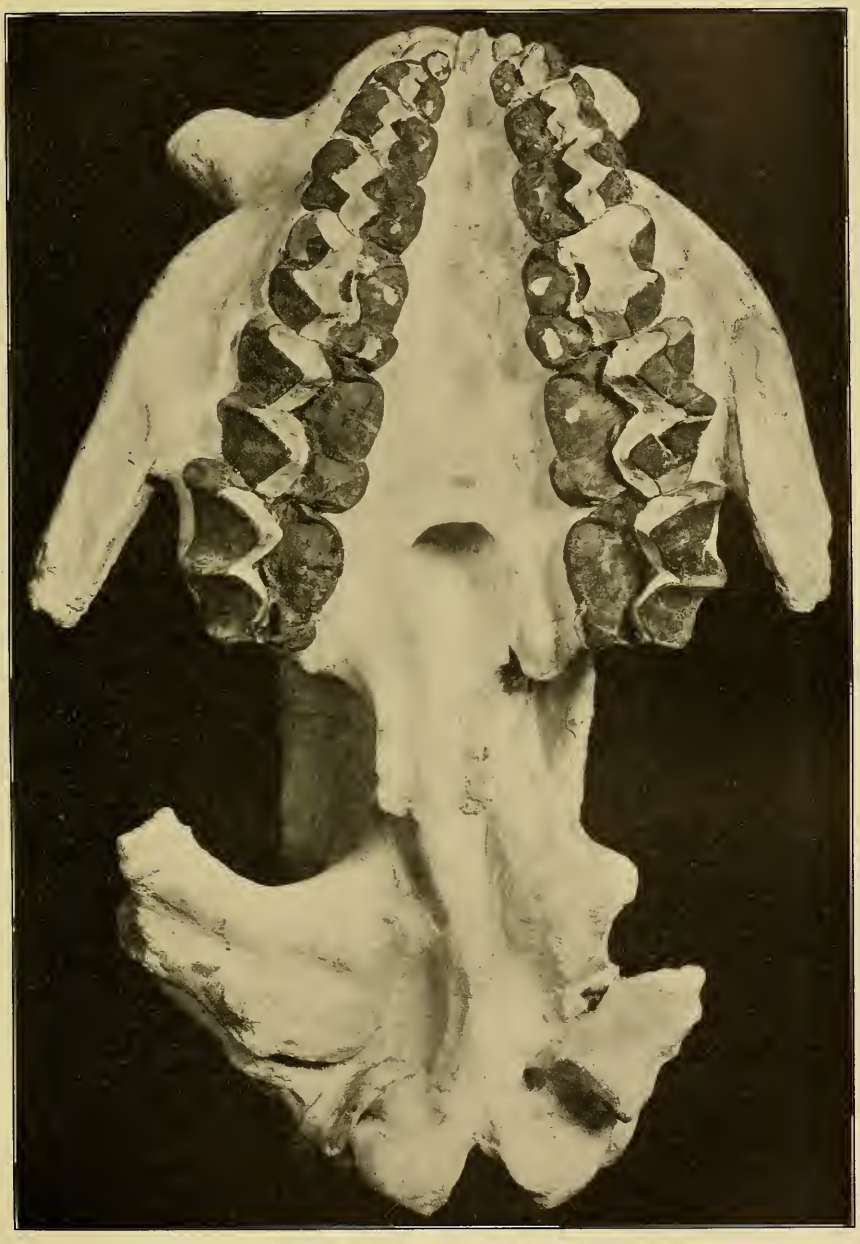
Female Skull Referred to Megacerops acer? (Type of Symborodon altirostris Cope)

Plate prepared under the direction of Professor Cope. (See p. 545)

Am. Mus. 6350, Horsetail Creek, northeastern Colorado, Chadron formation. Palatal view. One-third natural size. This figure is not as accurate as the photograph reproduced in Plate CLII, the characters of the teeth especially being very poorly portrayed. Affinity with *M. bucco* is indicated.



FEMALE SKULL OF MEGACEROPS ACER?, TYPE OF SYMBORODON ALTIROSTRIS



FEMALE SKULL OF MEGACEROPS ACER?

One-third natural size. (See p. 545, also Pls. CXLVI, CXLVII, and CLI.) Referred female skull (Am. Mus. 6350; type of *Symborodon altirostris* Cope), Horsetail Creek, northeastern Colorado, Chadron formation. The dentition reveals the generic characters mentioned in the explanation of Plate CXLV. Very clear evidences of close relationship with the skull figured in Plate CXLV, A

PLATE CLIII

PLATE CLIII

Type Skull of Megacerops bucco and Jaw of Brontops?

Plate prepared under the direction of Professor Cope. One-third natural size. (See p. 544)

A, *Megacerops* (*"Symborodon"*) *bucco*, type (Am. Mus. 6345a), Horsetail Creek, northeastern Colorado, Chadron formation. The skull is poorly preserved and is vertically crushed, thus rendering its specific affinities somewhat uncertain. The figure is rather unsatisfactory, especially in the form of the horns and nasals. Of the two cotype skulls referred to in Cope's original description of *Symborodon bucco* this one is taken as the lectotype, because upon it were based nearly all the measurements and specific characters listed by Cope.

B, Lower jaw of *Brontops?* (Am. Mus. 6345b), Horsetail Creek, northeastern Colorado, Chadron formation. Placed by Cope with the type skull of *Megacerops* (*"Symborodon"*) *bucco* but probably pertains to the genus *Brontops*. It differs from the supposed true *Megacerops* figured in Plate CLVIII, A, in general contour and in the possession of well-developed external cingula on the cheek teeth.

C, Undetermined jaw fragment from Colorado, referred by Cope to *Megacerops* (*"Symborodon"*) *bucco*. It may pertain to *Brontops*. (See Pl. CLVIII, B.)

TYPE SKULL OF MEGACEROPS BUCCO ("SYMBORODON") AND JAWS OF BRONTOPS

PLATE CLIV

PLATE CLIV

Type Skull of Megacerops bucco

Plate prepared under the direction of Professor Cope. One-half natural size. (See p. 544)

Megacerops (*"Symborodon"*) *bucco*, type (Am. Mus. 6345a), Horsetail Creek, northeastern Colorado, Chadron formation. Basal view. The dentition reveals generic affinity with the specimen figured in Plate CLII. The enormous size of the zygomata is alluded to in the name *"bucco"* ("one with swollen cheeks").

TYPE SKULL OF MEGACEROPS ("SYMBORODON") BUCCO

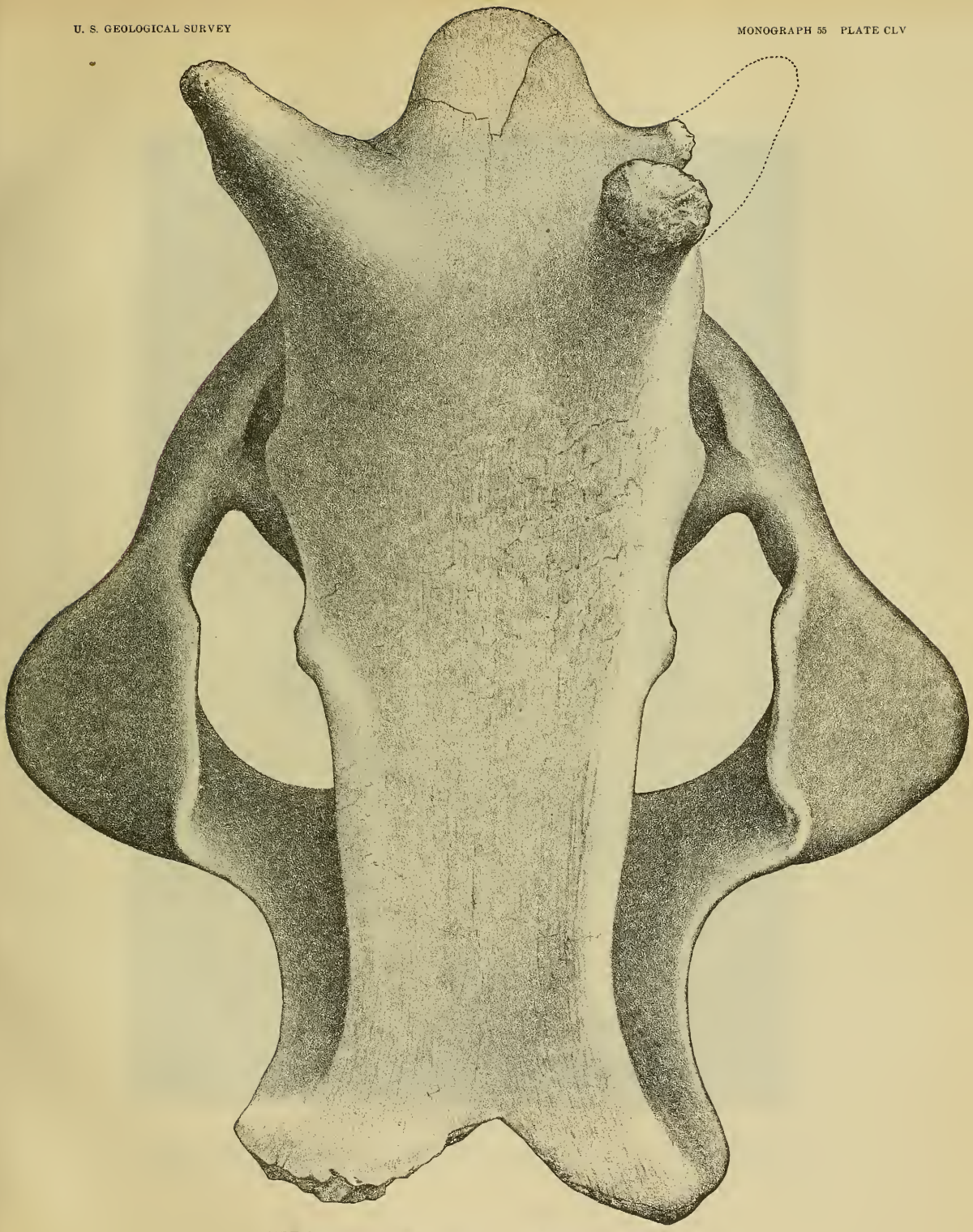
PLATE CLV

PLATE CLV

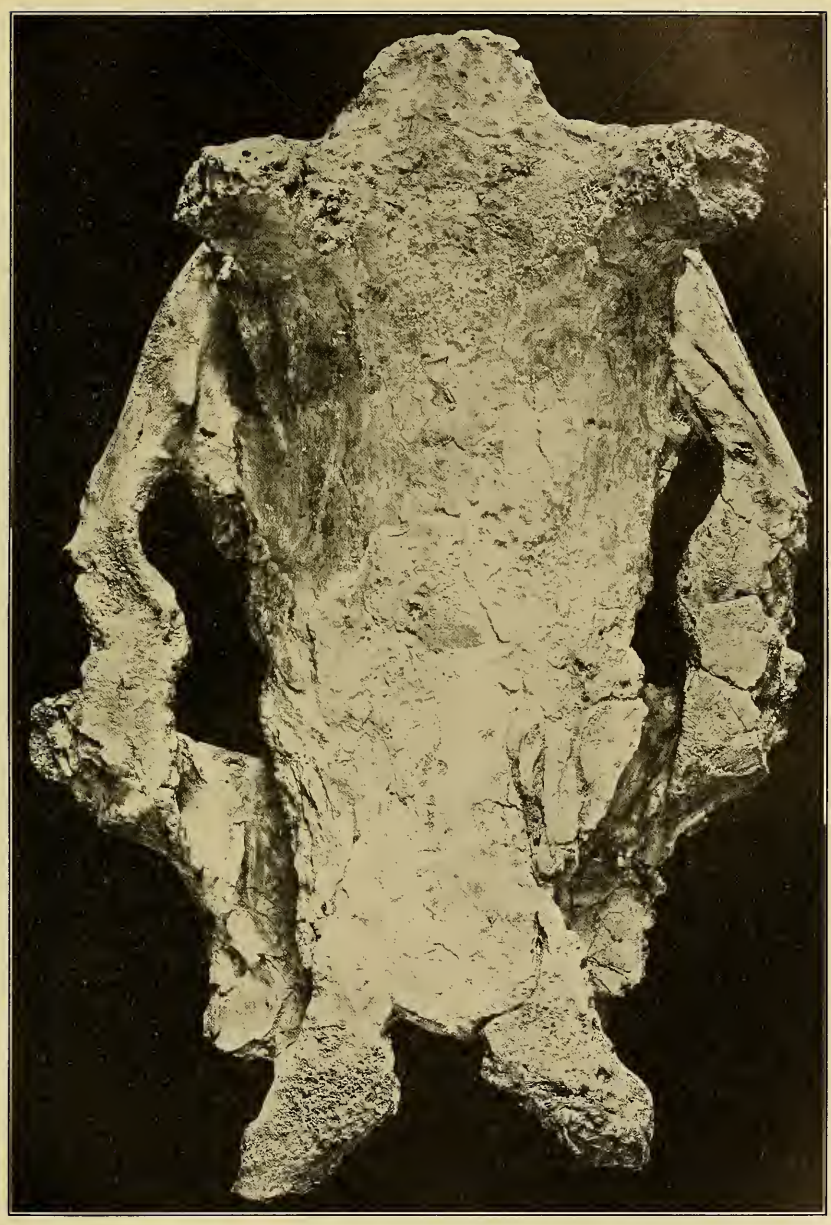
Type Skull of Megacerops bucco

Plate prepared under the direction of Professor Cope. One-third natural size. (See p. 544)

Megacerops (*"Symborodon"*) *bucco*, type (Am. Mus. 6345a), Horsetail Creek, northeastern Colorado, Chadron formation. The skull is crushed down, this somewhat increasing its apparent breadth. The horns are poorly preserved but may have resembled those of the skull figured in Plate CLVI. The enormous zygomata rival those of *Brontotherium*.



TYPE SKULL OF MEGACEROPS ("SYMBORODON") BUCCO



SKULL OF MEGACEROPS BUCCO?

Referred female skull, skull O[1] (Nat. Mus. 4705), Big Badlands, S. Dak., *Titanotherium* zone, upper levels of middle part (Hatcher). One-fourth natural size. Vertical crushing has probably emphasized the breadth and flatness. This is regarded by the author as a female skull of *M. bucco*

PLATE CLVII

PLATE CLVII

Skulls of Menodus, Brontotherium, and Megacerops and a Fragment of a Humerus

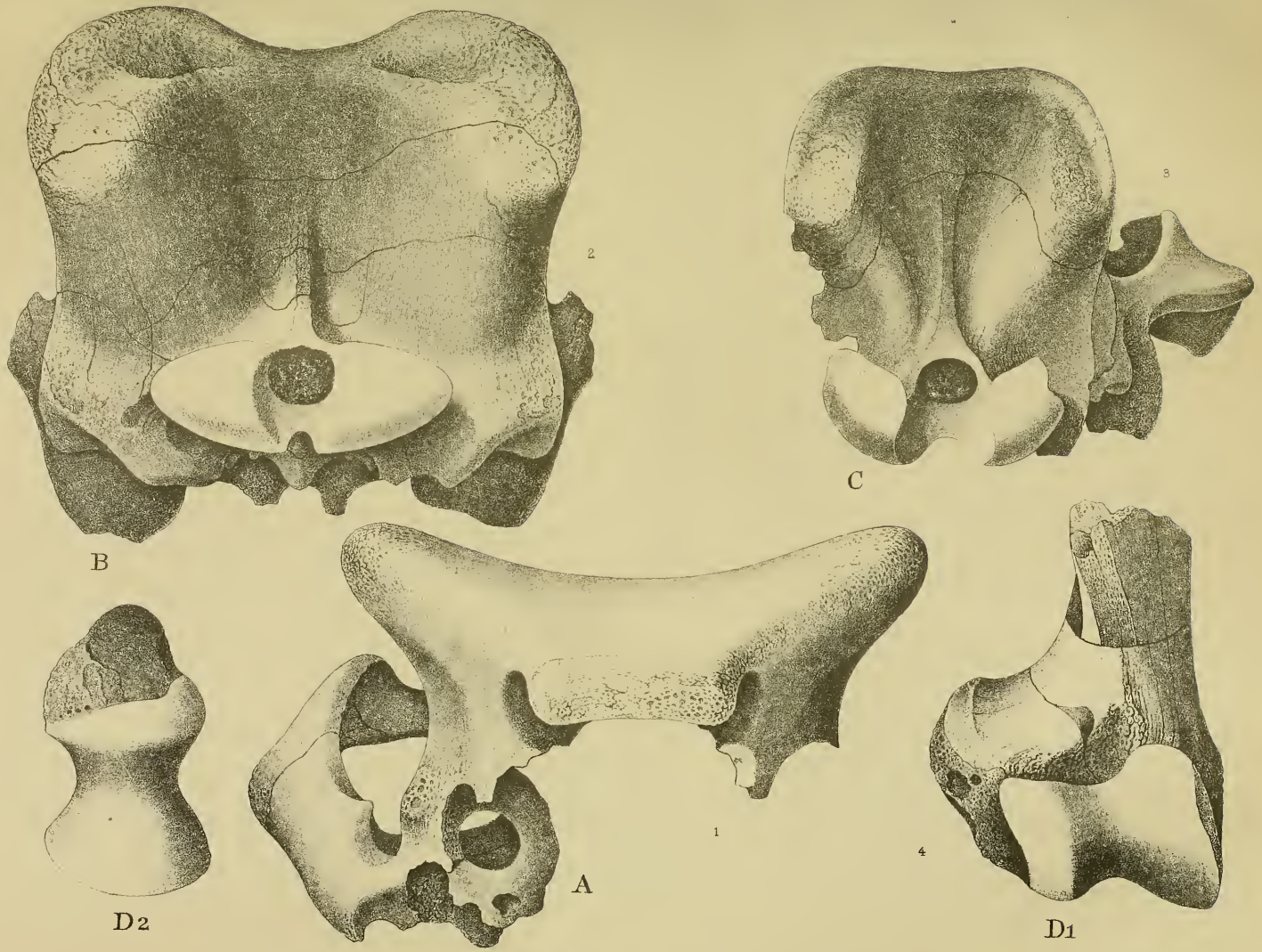
Plate prepared under the direction of Professor Cope. One-third natural size. (See pp. 529, 546, also Pls. CXXVIII, CXXIX, and CLXXXIII)

A, *Menodus trigonoceras*, type (Am. Mus. 6355), Horsetail Creek, northeastern Colorado, Chadron formation. Front view. This species was referred by Cope to "*Symborodon*."

B, Occiput referred to *Brontotherium curtum?* (Am. Mus. 6346), Horsetail Creek, northeastern Colorado, Chadron formation. This specimen was one of the cotypes of Cope's *Symborodon bucco* (see p. 212) but probably pertains to a large *Brontotherium*.

C, Female skull referred to *Megacerops acer?* (Am. Mus. 6349), Colorado, Chadron formation. Occipital view of a small skull regarded by Osborn as a female of *M. acer*.

D_1, D_2, Front and distal views of an undetermined humerus from the Chadron formation, Colorado.



SKULLS OF MENODUS, BRONTOTHERIUM, AND MEGACEROPS, AND A FRAGMENT OF HUMERUS

PLATE CLVIII

PLATE CLVIII

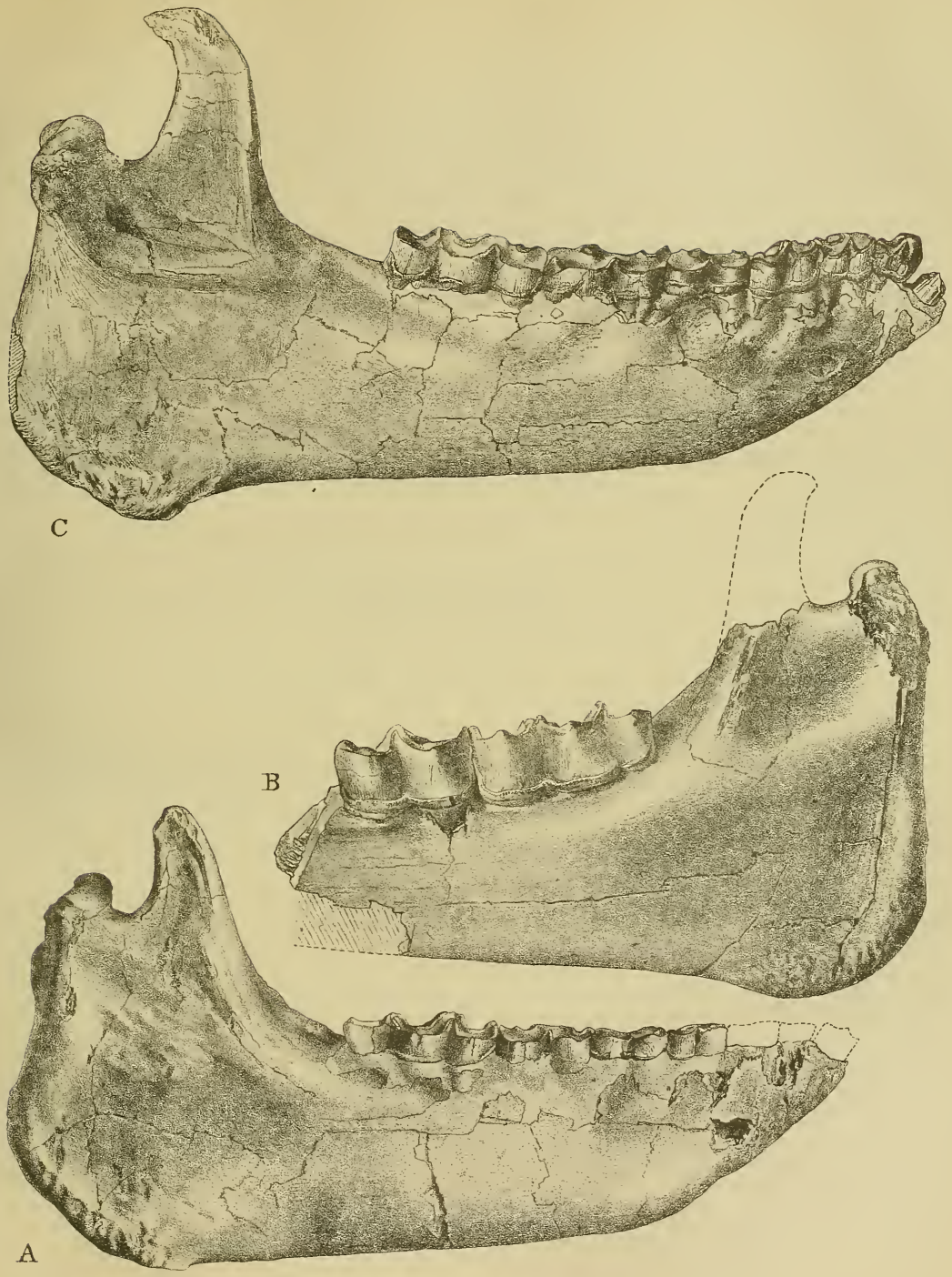
Jaws of Megacerops riggsi and Menodus torvus

Plate prepared under the direction of Professor Cope. One-third natural size. (See pp. 527, 550)

A, *Megacerops riggsi*, type (Am. Mus. 6364), Horsetail Creek, northeastern Colorado, Chadron formation. This jaw was referred by Cope to "*Symborodon acer*" but seems far too small to pertain to that species. It is in fact extremely small for an Oligocene titanothere. (See measurements, p. 242.) Reasons for referring it to *Megacerops* are the extremely short, thick horizontal ramus, low ascending ramus and coronoid, very short symphysis and premolars, molars with obsolete external cingula—characters which one would expect to find in the jaw of *Megacerops*.

B, Undetermined jaw fragment referred by Cope to "*S. bucco*." (See Pl. CLIII.)

C, *Menodus* ("*Symborodon*") *torvus*, type (Am. Mus. 6365), Horsetail Creek, northeastern Colorado, Chadron formation. This jaw is the genotype of *Symborodon* (see p. 210), Cope's original description of the genus having been based upon this jaw, although in his subsequent descriptions he erroneously included other material (jaws and skulls) belonging to other genera. The jaw seems to belong in the genus *Menodus*, as indicated by its general contour, measurements, absence of lower incisors, and robust external cingula on molars. The skulls which Cope referred to "*Symborodon*" appear not to be congeneric with this jaw but to pertain to Leidy's *Megacerops*.



TYPE JAWS OF MEGACEROPS RIGGSI AND MENODUS TORVUS

PLATE CLIX

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PLATE CLIX

Jaws of Megacerops riggsi and of Menodus torvus

Plate prepared under the direction of Professor Cope. One-third natural size. (See pp. 527, 550, also Pl. CLVIII)

A. Lower jaw of *Megacerops riggsi*, type (Am. Mus. 6364), Horsetail Creek, northeastern Colorado, Chadron formation. This shows the extremely short thick rami and short symphysis.

B, Unidentified jaw fragment from Colorado, referred by Cope to "*Menodus proutii*," which suggests that he intended to include under that term titanotheres with two incisors on each side.

C, Lower jaw of *Menodus* ("*Symborodon*") *torvus*, type (Am. Mus. 6365), Horsetail Creek, northeastern Colorado, Chadron formation. This jaw, the genotype of *Symborodon*, shows the long, slender rami and long symphyseal region characteristic of *Menodus* jaws.

TYPE JAWS OF MEGACEROPS RIGGSI AND MENODUS TORVUS

PLATE CLX

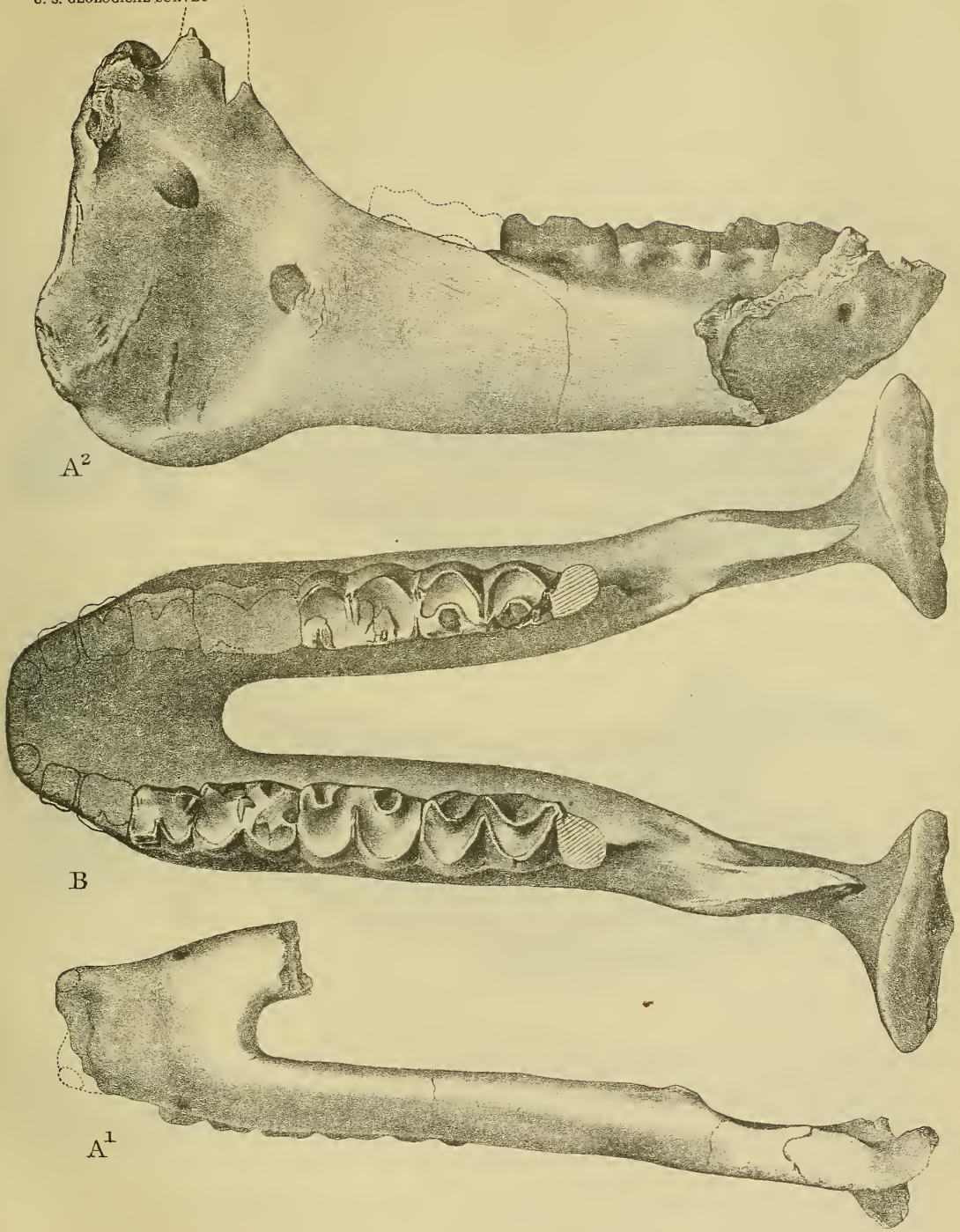
PLATE CLX

Jaws of Brontops sp. and of Megacerops riggsi

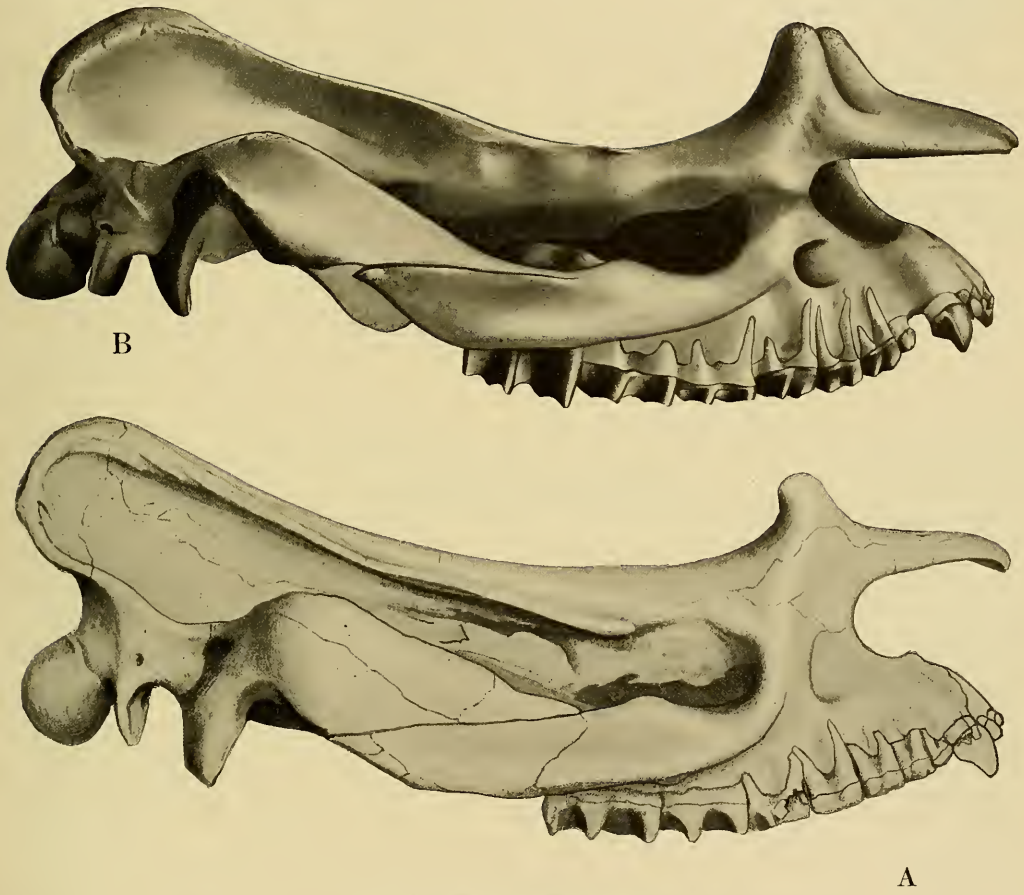
Plate prepared under the direction of Professor Cope. One-third natural size. (See p. 550)

A[1], A[2], Jaw referred to *Brontops?* sp. (Am. Mus. 6345b), Horsetail Creek, northeastern Colorado, Chadron formation. Incomplete lower jaw, seen from below and from the inner side; placed by Cope with the skull of "*Symborodon bucco*" (see Pl. CLIII) but probably pertaining to a different genus and species.

B, *Megacerops riggsi*, type (Am. Mus. 6364), Horsetail Creek, northeastern Colorado, Chadron formation. (See also Pls. CLVIII and CLIX.) This type lower jaw, seen from above, shows a short, thick symphysis, a short premolar series, and molars with external cingula obsolete—characters we should expect to find in *Megacerops*.



JAWS OF BRONTOPS SP. AND MEGACEROPS RIGGSI



SKULLS OF BRONTOTHERIUM LEIDYI

One-fourth natural size. (See p. 559.) A, Skull R, type (Nat. Mus. 4249), Big Badlands, S. Dak., Chadron formation, level middle A. Figure prepared under the direction of Professor Marsh. This oldest and most primitive member of the *Brontatherium* phylum foreshadows the later brontotheres in the flattened oval section of the horns, in the tapering decurved nasals, and especially in the progressive characters of the premolar dentition. (See Pl. CLXIII.) It is larger than the contemporary primitive members of the *Brontops* and *Menodus* phyla. B, Referred skull (Carnegie Mus. 93), Hat Creek, Nebr., Chadron formation, level lower A ("15 or 20 feet from bottom of lower beds"—J. B. Hatcher). Figure prepared under the direction of the author. This well-preserved skull has the horns a little longer than in the type. Male sex is indicated by the large size of the canines

PLATE CLXII

PLATE CLXII

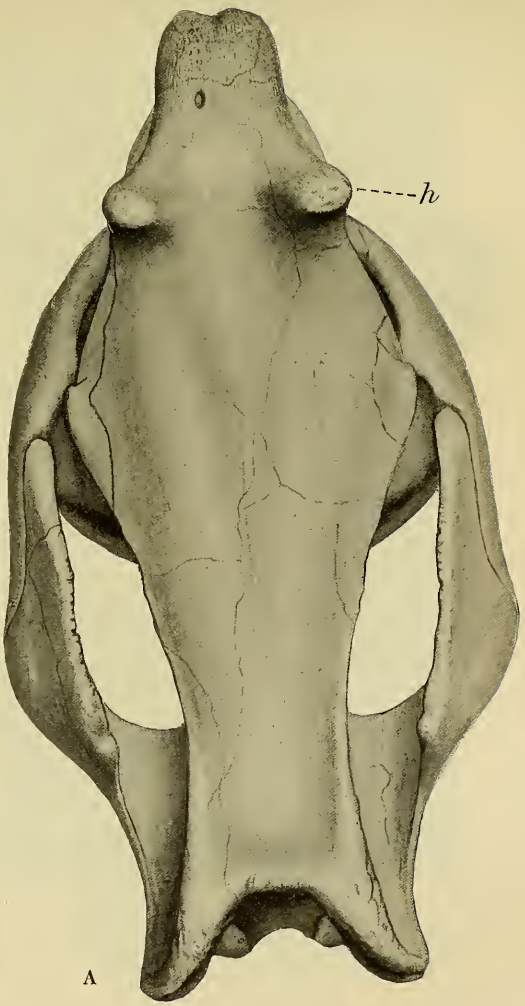
Skulls of Brontotherium leidyi

One-fourth natural size. (See p. 559)

A, Skull R, type (Nat. Mus. 4249), Big Badlands, S. Dak., Chadron formation, level middle A. Figure prepared under the direction of Professor Marsh. The nasals are long and tapering, the small horns are flattened posteriorly; the skull top is long, and the zygomata slender.

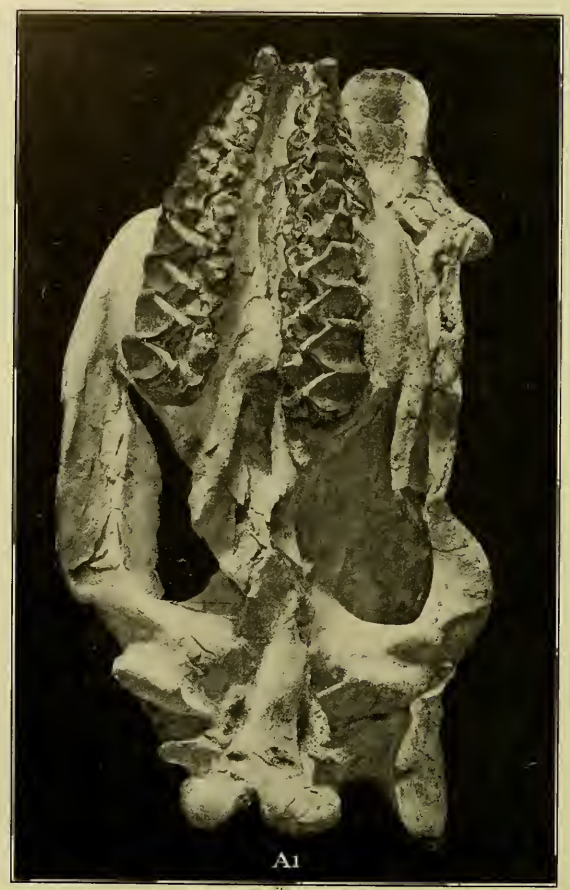
B, Referred skull (Carnegie Mus. 93), Hat Creek, Nebr., Chadron formation, level lower A ("15 or 20 feet from bottom of lower beds"—J. B. Hatcher). This and the preceding skull show that the *Brontotherium* phylum was already well differentiated from the other genera at the period when the lower "*Titanotherium* beds" were laid down.

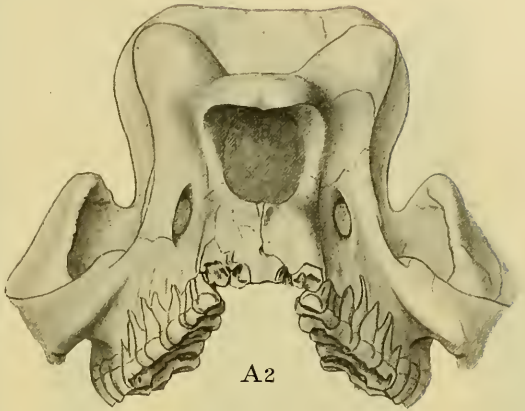
B

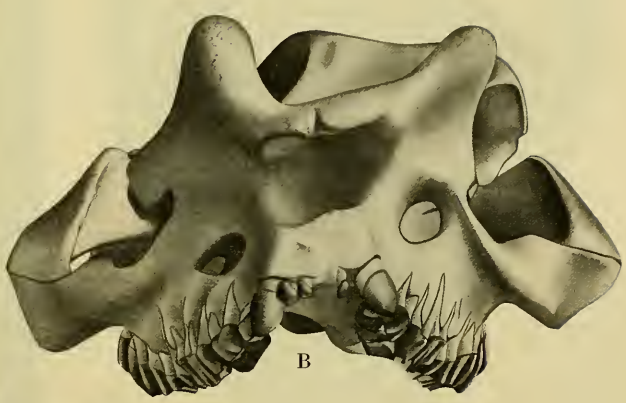


A

SKULLS OF BRONTOTHERIUM LEIDY







SKULLS OF BRONTOTHERIUM LEIDYI

(See p. 559, also Pls. CLXI and CLXII.) A_1, Skull R, type (Nat. Mus. 4249), Big Badlands, S. Dak., Chadron formation, level middle A. Figure prepared under the direction of the author. One-fifth natural size. The left upper tooth row is crushed in toward the opposite side. The progressive premolar dentition is fully characteristic of *Brontotherium*, even in this oldest stage, which indicates a wide separation from the Menodontinae. The canines are short and swelling; they retain, however, the internal basal cingulum which is lost in later brontotheres. P^1 is very small; p^2, p^3, and p^4 are very progressive, with very large and circular internal cusps and faint or vestigial external cingula. The large, broad molars have well-developed protostyles and jutting hypocones. A_2, The same. Figure prepared under the direction of Professor Marsh. One-fourth natural size. This illustrates the small, divergent horns, the deep zygomata, and the alveoli for i^3. B, Referred skull (Carnegie Mus. 93), Hat Creek, Nebr., Chadron formation, level lower A ("15 or 20 feet from bottom of lower beds"—J. B. Hatcher). Figure prepared under the direction of the author. One-fourth natural size. This skull, which is somewhat crushed downward, shows well the large incisors and swollen canines that are characteristic of the genus

SKULL AND JAW OF BRONTOTHERIUM LEIDYI

One-fourth natural size. (See p. 559.) Referred skull (Carnegie Mus. 93), Hat Creek, Nebr., Chadron formation, level lower A ("15 or 20 feet from bottom of lower beds"—J. B. Hatcher). The skull is somewhat crushed downward. The chief characters of this skull have been described above. (See Pl. CLXI.) This view exhibits well the stout incisors and canines and the upward curvature of the premolar series. The associated lower jaw has a very shallow horizontal ramus (slightly crushed) and a slender ascending ramus. The canine is massive and procumbent, the "chin" concave. The lower cheek teeth lack the external cingulum

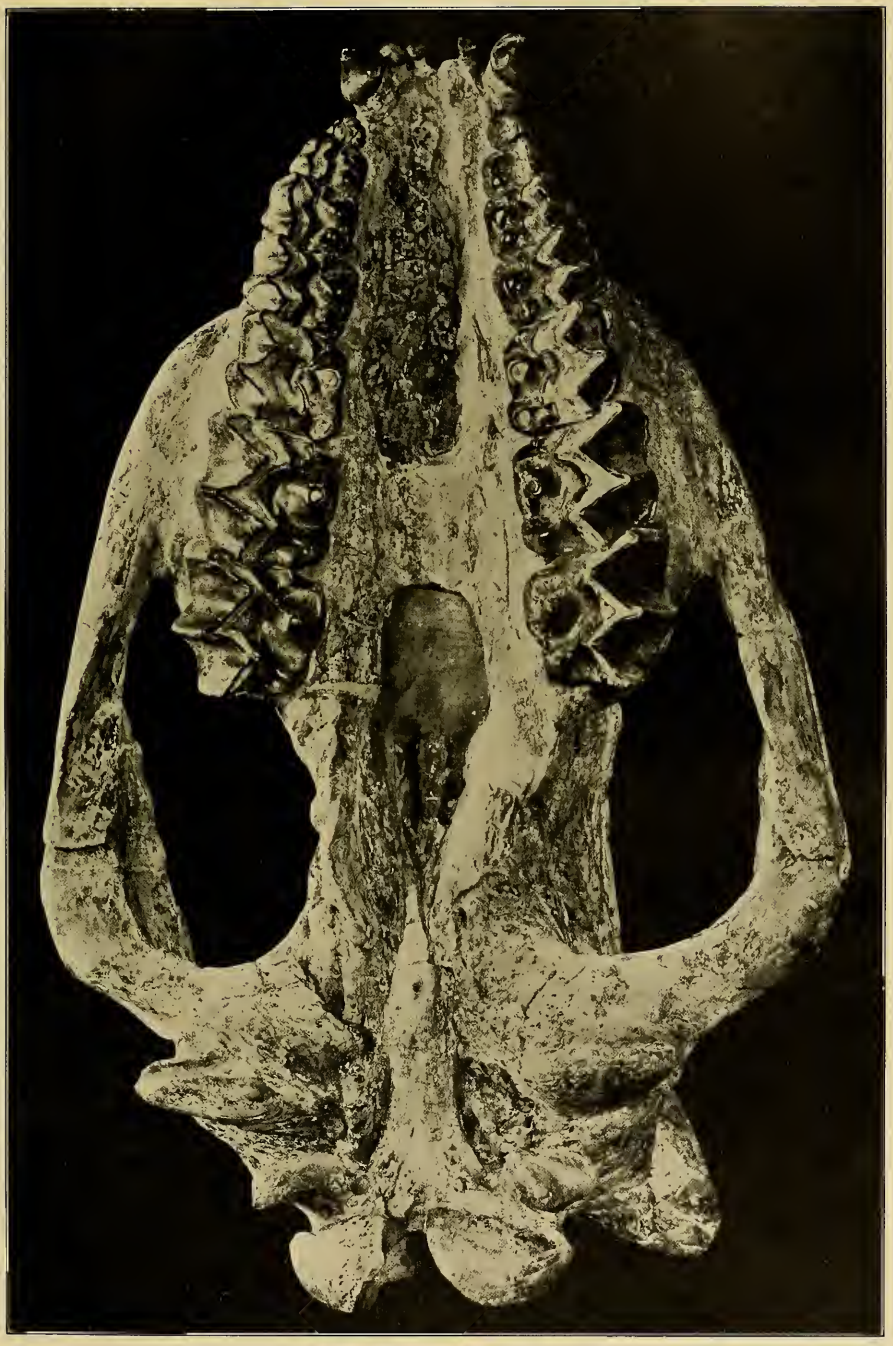
PLATE CLXV

PLATE CLXV

Skull of Brontotherium leidyi

One-third natural size. (See p. 559)

Referred skull (Carnegie Mus. 93), Hat Creek, Nebr., Chadron formation, level lower A ("15 or 20 feet from bottom of lower beds"—J. B. Hatcher). This view exhibits the very progressive *Brontotherium* characters of the dentition in this oldest known member of the phylum, especially the massive swollen canines, the large incisors, the broad submolariform premolars with circular internal cusps, the vestigial external cingula, the blunt internal cingula, and the wide molars, with stout protostyles and protuberant hypocones. In measurements the dentition nearly equals that in certain specimens of *B. hatcheri*, and the basilar skull length is only 5 centimeters less



SKULL OF BRONTOTHERIUM LEIDYI

PLATE CLXVI

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PLATE CLXVI

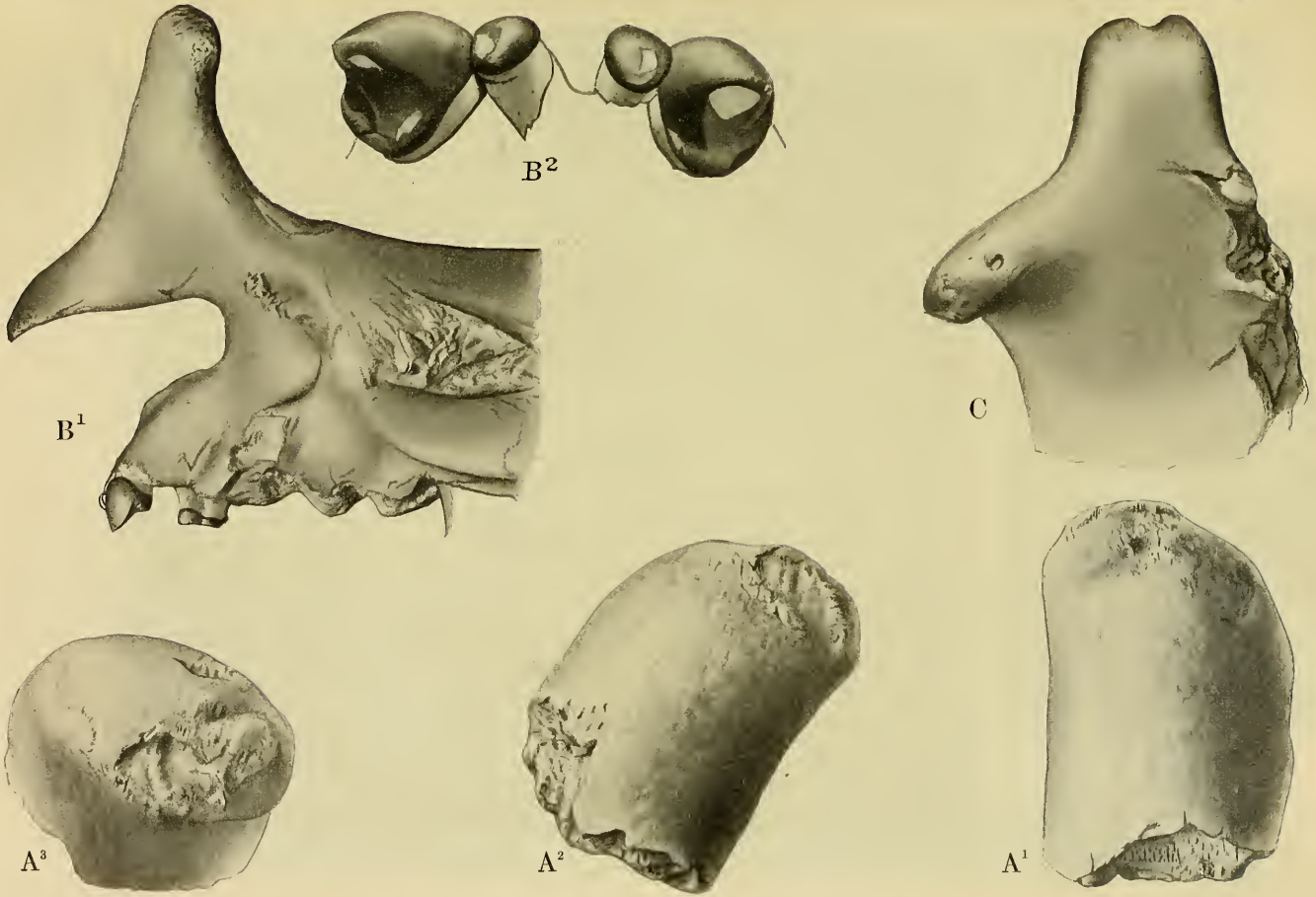
Type and Referred Specimens of Brontotherium hypoceras

(See p. 562)

A, Horn, type of *Brontotherium hypoceras* (Am. Mus. 6361), northeastern Colorado, Chadron formation. Natural size. Of the type of this species several skull fragments are all that remain; among these is the tip of the right horn, here shown in the front (A^1), back (A^2), and top (A^3) views. The horn has a compressed oval section, as in brontotheres, but is very small.

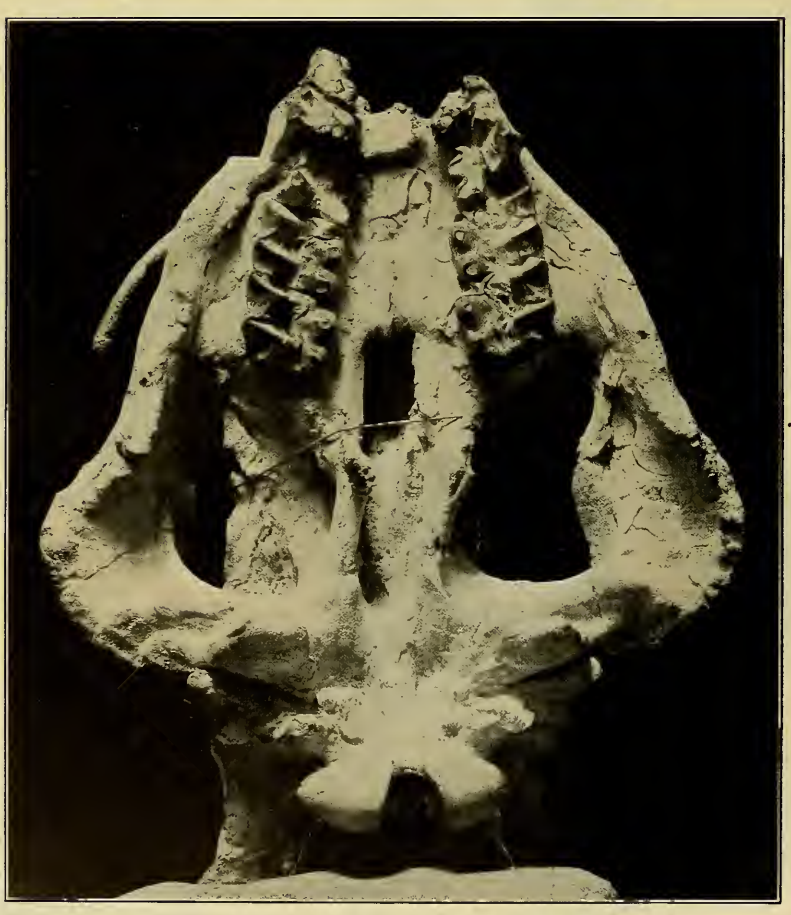
B^1, Skull referred to *Brontotherium hypoceras?*, neotype (Nat. Mus. 4273), skull l, Indian Draw, Big Badlands, S. Dak., *Titanotherium* zone, probably level upper A (Hatcher). One-third natural size. The horn tip closely resembles that of the type of *B. hypoceras*. B^2, The same. Upper front teeth, natural size. The dental measurements are about the same as in *B. leidyi*, and this may represent a more progressive mutation from that species. The extreme forward position of the horns is emphasized by crushing. The massive swollen canines and large incisor are of *Brontotherium* type. The inner incisors have probably dropped out as the animal grew old.

C, Horn and nasal referred to *Brontotherium hypoceras* (Nat. Mus. 4940), skull m, Indian Draw, Big Badlands, S. Dak., *Titanotherium* zone, level upper A (Hatcher). One-third natural size. This specimen is referred to *B. hypoceras* on account of the similarity in the horn and nasals.



TYPE AND REFERRED SPECIMENS OF BRONTOTHERIUM HYPOCERAS

A_2



A_1

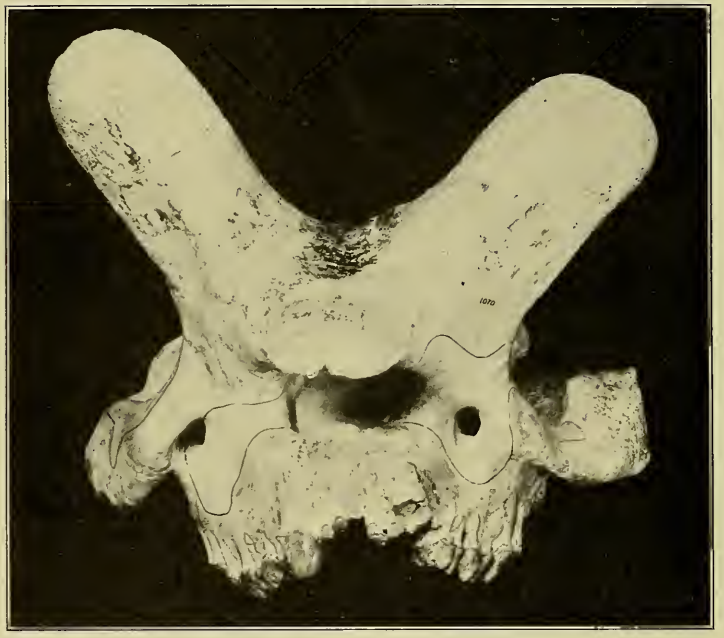
TYPE SKULL OF BRONTOTHERIUM HATCHERI

One-fifth natural size. (See p. 563.) Skull a, type (Nat. Mus. 1216), Big Badlands, S. Dak. (?Corral Draw), *Titanotherium* zone, level upper B (Hatcher). A_1, Palatal view. The grinding teeth conform to the *Brontotherium* pattern, which, apart from size, appears to show little variation in the different species. A_2, Front view of horns. The horns in this animal are considerably shorter than those of the typical B. *gigas* (which is recorded from a higher level), and they are also less flattened, especially at the base; the connecting crest is low

TYPE SKULL OF BRONTOTHERIUM HATCHERI

One-fourth natural size. (See p. 563.) Skull a, type (Nat. Mus. 1216), Big Badlands, S. Dak. (?Corral Draw), *Titanotherium* zone, level upper B (Hatcher). Vertical crushing may have emphasized the great breadth of this skull, and the horns have been crushed back above the orbits. The thick horns are not much flattened. The supratemporal crests have parallel sides, as in many Brontotheriinae, whereas in the Menodontinae they curve inward in the parietal region. The buccal swellings are almost as large as in the most advanced species of the genus

A_1



A_2

SKULL REFERRED TO BRONTOTHERIUM HATCHERI

(See p. 563.) Am. Mus. 1070, Hat Creek Badlands, Nebr., Chadron formation. A^1, Upper dentition. One-third natural size. The generic characters are well shown; incisors large, canines swollen, premolars wide and submolariform with large circular internal cusps, external cingula absent, internal cingula thick and wrinkled, molars wide, with large protostyles and hypocones, cingula vestigial. The molars of the right side have been elongated by crushing. A^2, Front view of skull. One-fourth natural size. The horns are short and thick, with low connecting crest. The infra-orbital canal, as in other brontotheres, is subcircular. The dimensions of the jaw belonging with this skull (Pl. CLXVIII) do not differ greatly from those of the type jaw of *Brontotherium gigas* Marsh

PLATE CLXX

PLATE CLXX

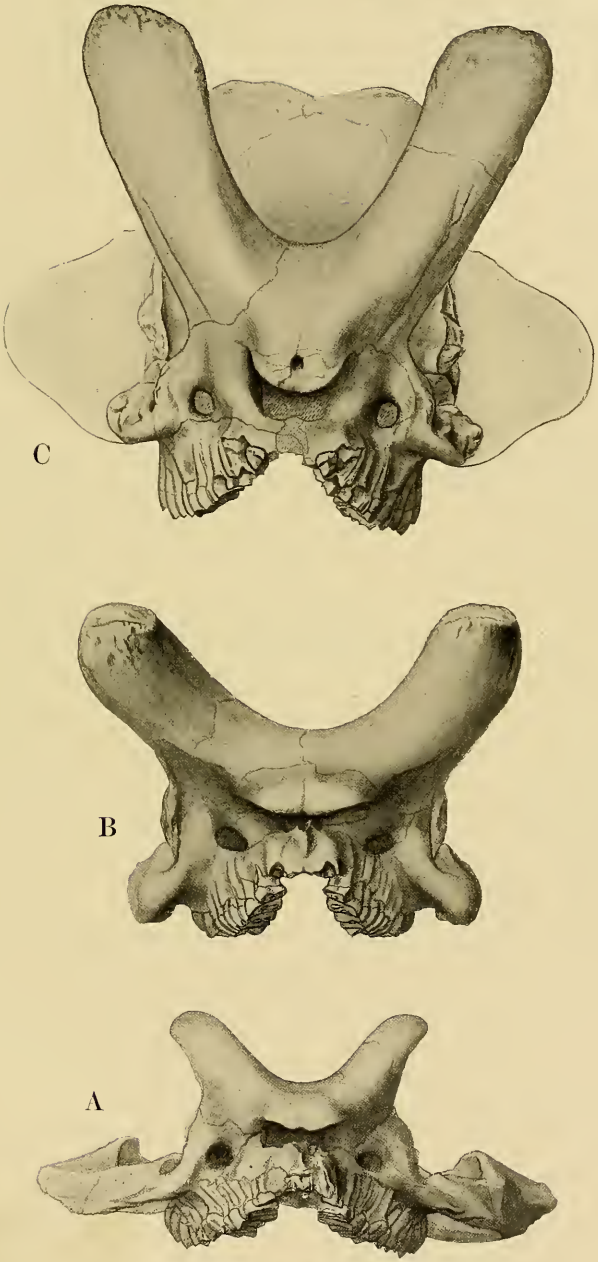
Front View of Skulls of Three Brontotheres

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See pp. 562, 563, 568)

A, Skull referred to *Brontotherium hypoceras?* (Nat. Mus. 4702), skull K^1, South Dakota, doubtfully recorded from the lower part of the *Titanotherium* zone (Hatcher). This skull has small slender horns, but the grinding teeth are as large as in certain skulls referred to *B. gigas*. The width across the zygomata is probably increased by flattening.

B, Skull referred to *Brontotherium hatcheri* (Nat. Mus. 4255), skull Q^1, South Dakota, *Titanotherium* zone, level upper B (Hatcher), middle part of *Titanotherium* zone. The horns are a little longer than in the type of *B. hatcheri* but considerably shorter and less flattened than in the typical *B. gigas*. The zygomata are not shown.

C, Skull referred to *Brontotherium gigas* (Yale Mus. 12061; type skull of *Titanops elatus* Marsh), South Dakota, exact locality not published, Chadron formation. The horns are long and the nasals narrow. This stage is characteristic of the upper part of the *Titanotherium* zone (Hatcher).



FRONT VIEW OF SKULLS OF THREE BRONTOTHERES

PLATE CLXXI

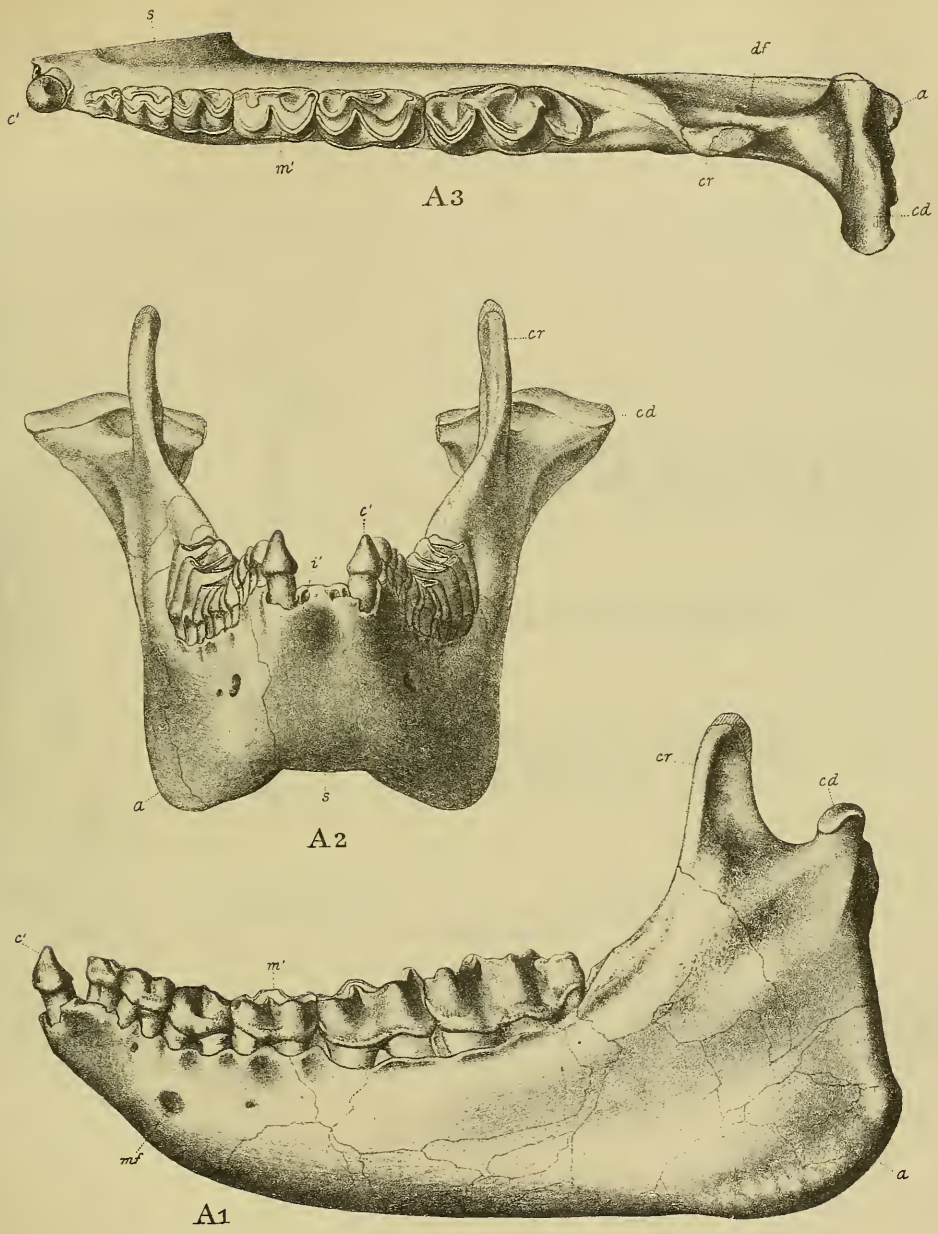
PLATE CLXXI

Type Jaw of Brontotherium gigas

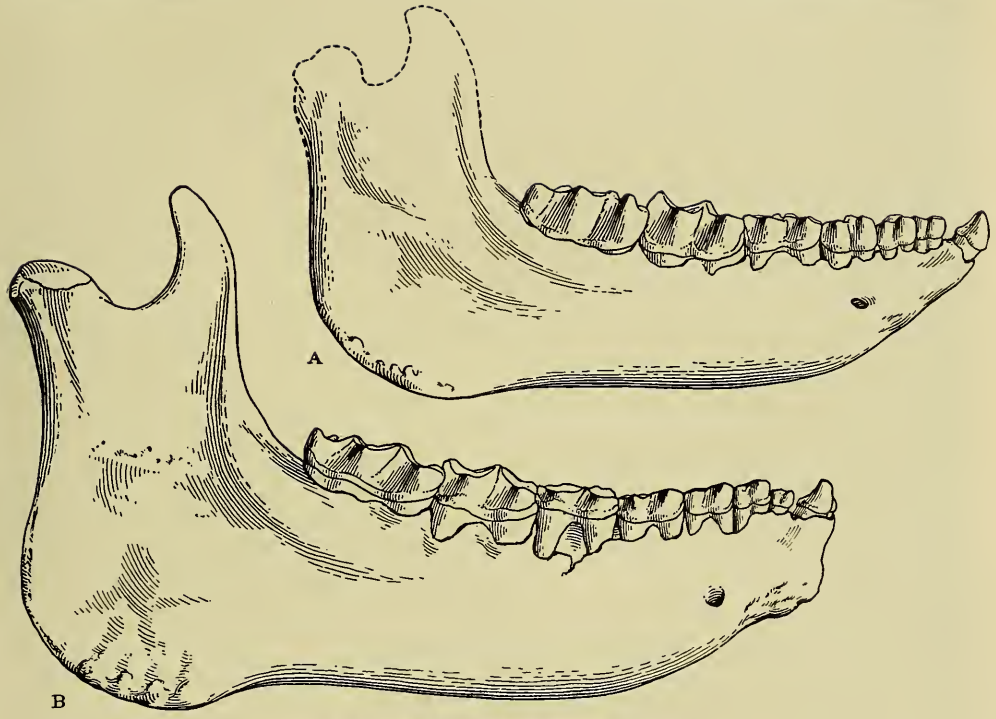
Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 568)

Yale Mus. 12009, Colorado, Chadron formation. A_1, Outer side view; A_2, front view; A_3, crown view of dentition. This important genotype, described in June, 1873, together with other jaws and limb bones, formed the material which Marsh used in defining the genus *Brontotherium*, family Brontotheriidae, and it was also the first representative of the flat-horned species which were later described under the generic name *Titanops*.

The skull subsequently named by Marsh *Brontotherium ingens* does not belong in the same genus with *B. gigas* and is now referred to *Menodus*. Generic characters shown in this jaw are the shallow chin, the swollen canines, the lack of external cingula on the premolars. P_1 has been shed; the alveoli for incisors 1 and 2 of the left side are visible. The jaw belonged to a somewhat young adult. The measurements do not differ much from those of jaws called *Brontotherium hatcheri* by Osborn.



TYPE JAW OF BRONTOTHERIUM GIGAS



JAWS OF TWO SPECIES OF BRONTOTHERIUM

One-fourth natural size. (See pp. 565, 573.) A, Jaw referred to *Brontotherium hatcheri*? (Am. Mus. 1070), Hat Creek badlands, Nebr., Chadron formation. This jaw belongs with the skull shown in Plate CLXIX. In the measurements of the teeth this specimen is a little larger than the type of B. *gigas*. The latter, however, is curved upward in front and does not project posteriorly. B, Jaw referred to *Brontotherium medium*? (Am. Mus. 1051), Cheyenne River badlands, S. Dak., Chadron formation. This huge jaw represents one of the largest known titanotheres. Its measurements are given on page 569. It differs from other known brontotheres in having an angulate chin and in the large size of the teeth

SKULL OF BRONTOTHERIUM GIGAS ELATUS

One-fourth natural size. (See p. 568, also Pl. CLXXIV.) Skull referred to *Brontotherium gigas* (Am. Mus. 492), Cheyenne River badlands, S. Dak., Chadron formation. The horns are much longer than in *B. hatcheri* but not so slender as in the type of *Titanops elatus*. The width and flatness of the buccal expansion of the zygomata are somewhat increased by crushing

SKULL OF BRONTOTHERIUM GIGAS ELATUS

One-fifth natural size. (See p. 568, also Pl. CLXXIII.) Skull referred to *Brontotherium gigas* (Am. Mus. 492), Cheyenne River Badlands, S. Dak., Chadron formation. This is a typical brontothere, probably from the upper part of the *Titanotherium* zone. The horns and nasals are thicker than in the type of *Titanops elatus* (Pl. CLXXV); the nasals longer than in the types of *B. medium* and *B. curtum*. The vertical diameters, especially of the orbit and of the anterior narial incisure, have been lessened by crushing. The upper teeth of this skull are shown in Plate LXXXII, D. The jaw here shown with this skull (Am. Mus. 1051) belonged to a larger animal. (See Pl. CLXXII, B)

PLATE CLXXV

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PLATE CLXXV

Skull of Brontotherium gigas elatus

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 570)

Skull referred to *Brontotherium gigas* (Yale Mus. 12061; type of *Titanops elatus* Marsh), South Dakota, Chadron formation, probably upper levels. The skull is a little crushed downward in front. Marsh did not recognize the generic relationship of this animal with his *Brontotherium gigas* type jaw, and therefore he established for it the new genus *Titanops*. In 1902 Osborn referred this skull and jaw to *Brontotherium gigas*, the type of which belonged to a somewhat younger animal. The present jaw is a little larger than the type *B. gigas* jaw, but this may possibly be due to greater age rather than to specific differences.

SKULL OF BRONTOTHERIUM GIGAS ELATUS

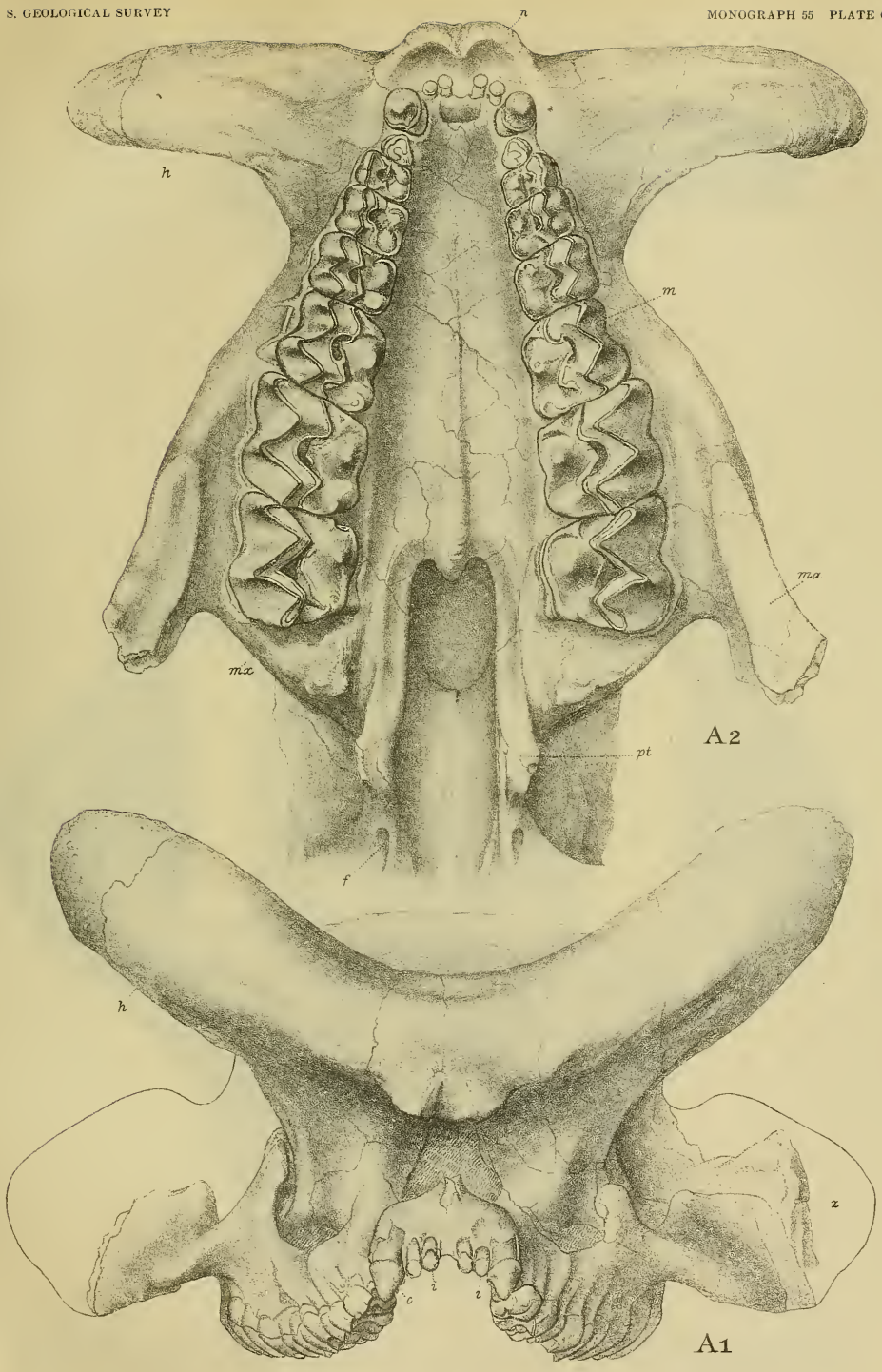
PLATE CLXXVI

PLATE CLXXVI

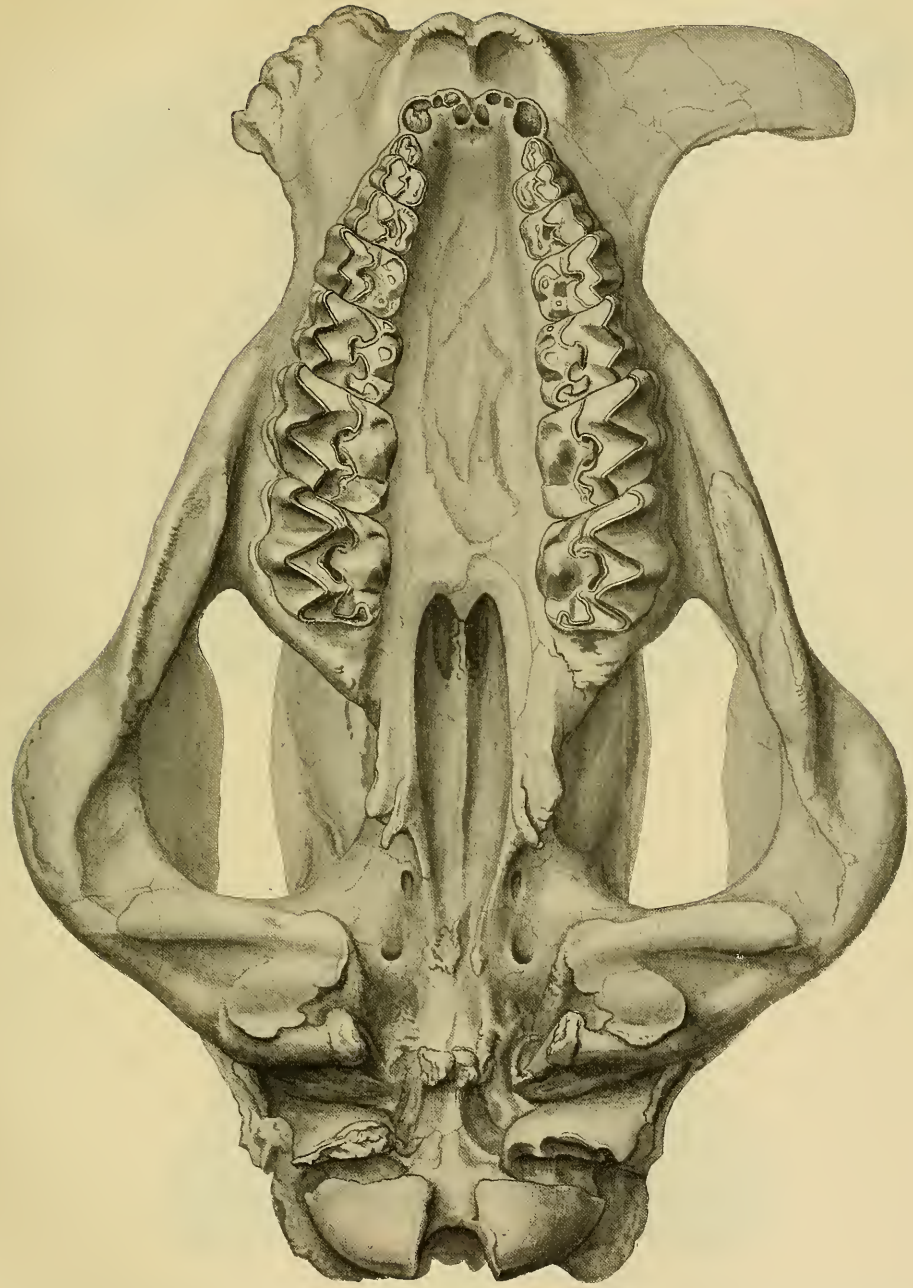
Type Skull of Brontotherium medium

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 573)

Skull w, type (Nat. Mus. 4256), Big Badlands, S. Dak. (?Indian Draw), Chadron formation, level upper C. A_1, Front view; A_2, palatal view. The specific name *medium* was given in allusion to the intermediate length of the nasals, which are shorter than in the type of *elatus* but longer than in type of *curtum*. (See Pls. CLXXV and CLXXVII.) The horns are of the same general form as those of *B. curtum* and *B. platyceras*, though not quite so flat. The generic characters noted above (Pls. CXXXIII and CLXIII) are well shown in the dentition.

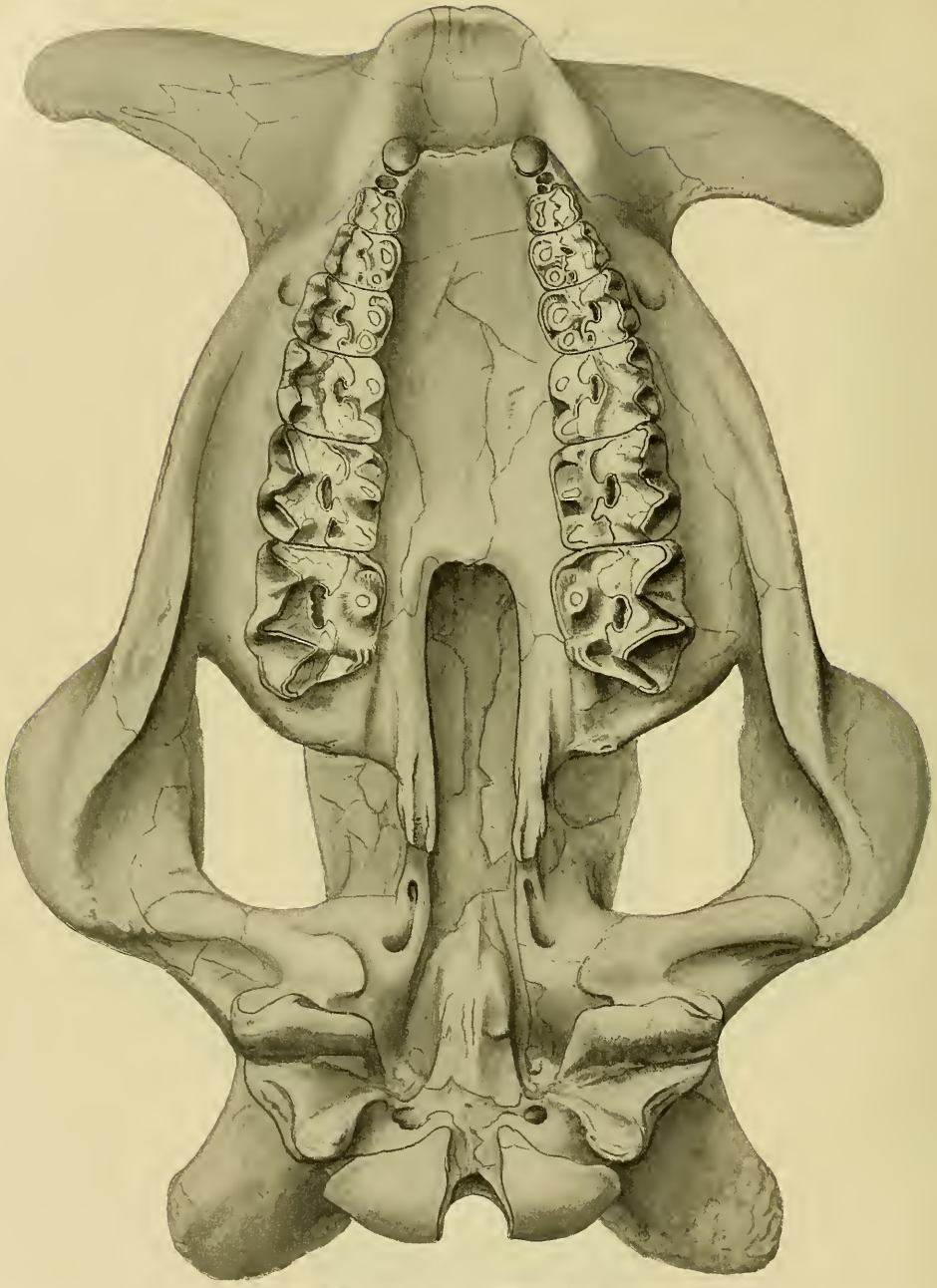


TYPE SKULL OF BRONTOTHERIUM MEDIUM



SKULL OF BRONTOTHERIUM CURTUM

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 575.) Skull q (Nat. Mus. 4946), Big Badlands, S. Dak. (?Indian Draw), Chadron formation, level upper C (Hatcher). This skull is somewhat more progressive than the type of B. *medium*, with broader zygomatic arches, flatter horns, and more abbreviated nasals. The dental series is a little smaller. The right horn has been broken off and healed during life (See Pl. CLXXXV, B)



TYPE SKULL OF BRONTOTHERIUM CURTUM

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 575, also Pl. CLXXIX.) Yale Mus. 12013, type of *Brontotherium* ("*Titanops*") *curtum* Marsh, Colorado, Chadron formation, upper beds (Hatcher). This stage is very near the culmination of the *Brontotherium* phylum. The nasals are very short, the horns long and much flattened, the buccal expansions of the zygomata enormous. The incisor alveoli are not preserved in this specimen. The cheek teeth conform to the *Brontotherium* pattern already described. (See Pl. CLXV)

PLATE CLXXIX

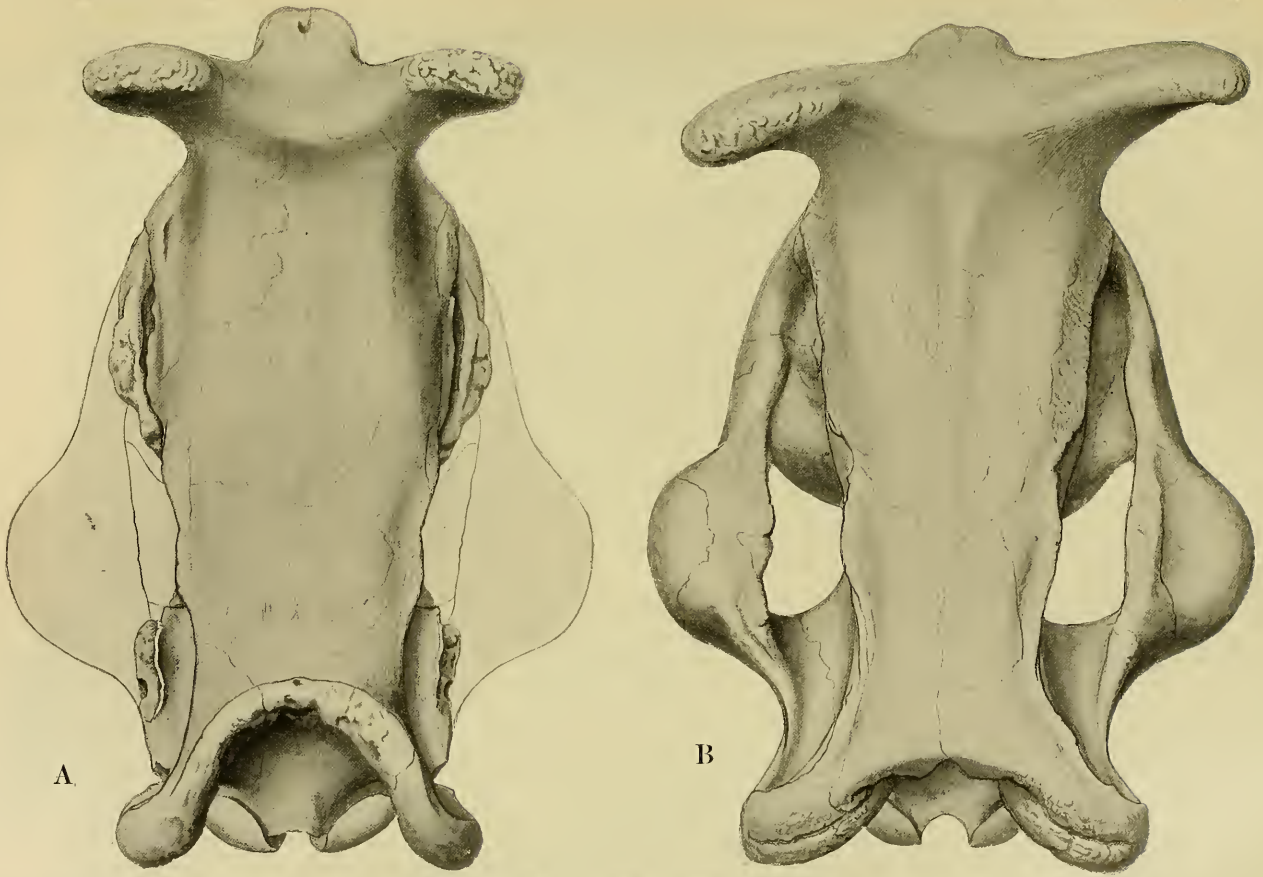
PLATE CLXXIX

Type Skull of Brontotherium curtum

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 575, also Pl. CLXXVIII)

Yale Mus. 12013, type of *Brontotherium* (*"Titanops"*) *curtum* Marsh, Colorado, Chadron formation, upper beds (Hatcher). A_1, Side view. This shows the marked flattening and forward position of the horns, the shortness of the nasals, the high narial incisure, and the massive zygomata. A_2, Front view of horns. It is possible that this species is the same as the *Brontotherium platyceras* of Osborn; if so the name *platyceras* would have priority over *curtum*. (See Pl. CLXXXI.)

TYPE SKULL OF BRONTOTHERIUM ("TITANOPS") CURTUM



TYPE SKULLS OF BRONTOTHERIUM MEDIUM AND B. CURTUM

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See pp. 573, 575, also Pls. CLXXVI, CLXXVIII, and CLXXIX.) A, *Brontotherium medium*, skull w, type (Nat. Mus. 4256), Big Badlands, S. Dak. (?Indian Draw), Chadron formation, level upper C (Hatcher). The top view shows that in comparison with *B. curtum* (B) the type of *B. medium* is less specialized in having smaller and less flattened horns, less abbreviated nasals, and less expanded zygomata. The character of the occipital crest, as here figured, is peculiar to this skull. B, *B. curtum*, type (Yale Mus. 12013), Colorado, Chadron formation, upper beds (Hatcher). Notwithstanding the great absolute width of the skull top, the anteroposterior dimension is proportionally still greater, so that if it were not for the expansion of the zygomata these *Brontotherium* skull tops would appear to be dolichocephalic

SKULL OF BRONTOTHERIUM PLATYCERAS

Photograph furnished by the Field Museum through the courtesy of Mr. E. S. Riggs. One-fifth natural size. (See p. 581, also Pl. CLXXXII.) Referred skull (Field Mus. 12161), Phinney Spring, S. Dak., Chadron formation, upper beds. This superb skull is the largest titanothere known and represents the culminating stage of the *Brontotherium* phylum. The skull is much longer than in the American Museum specimen (No. 1448) of this species, but the horns are shorter. The nasals are very short, narrow, and directed downward. In the width of the horns near the summit this skull approaches the type of *B. ramosum*

SKULL OF BRONTOTHERIUM PLATYCERAS

Photograph furnished by the Field Museum through the courtesy of Mr. E. S. Riggs. One-fifth natural size. (See p. 581, also Pl. CLXXXI.) Referred skull (Field Mus. 12161), Phinney Spring, S. Dak., Chadron formation, upper beds. The top view shows well the very elongate straight-sided skull top and the widely divergent, very flattened horns with their high connecting crest. The zygomatic width and expansion are foreshortened in the photograph

PLATE CLXXXIII

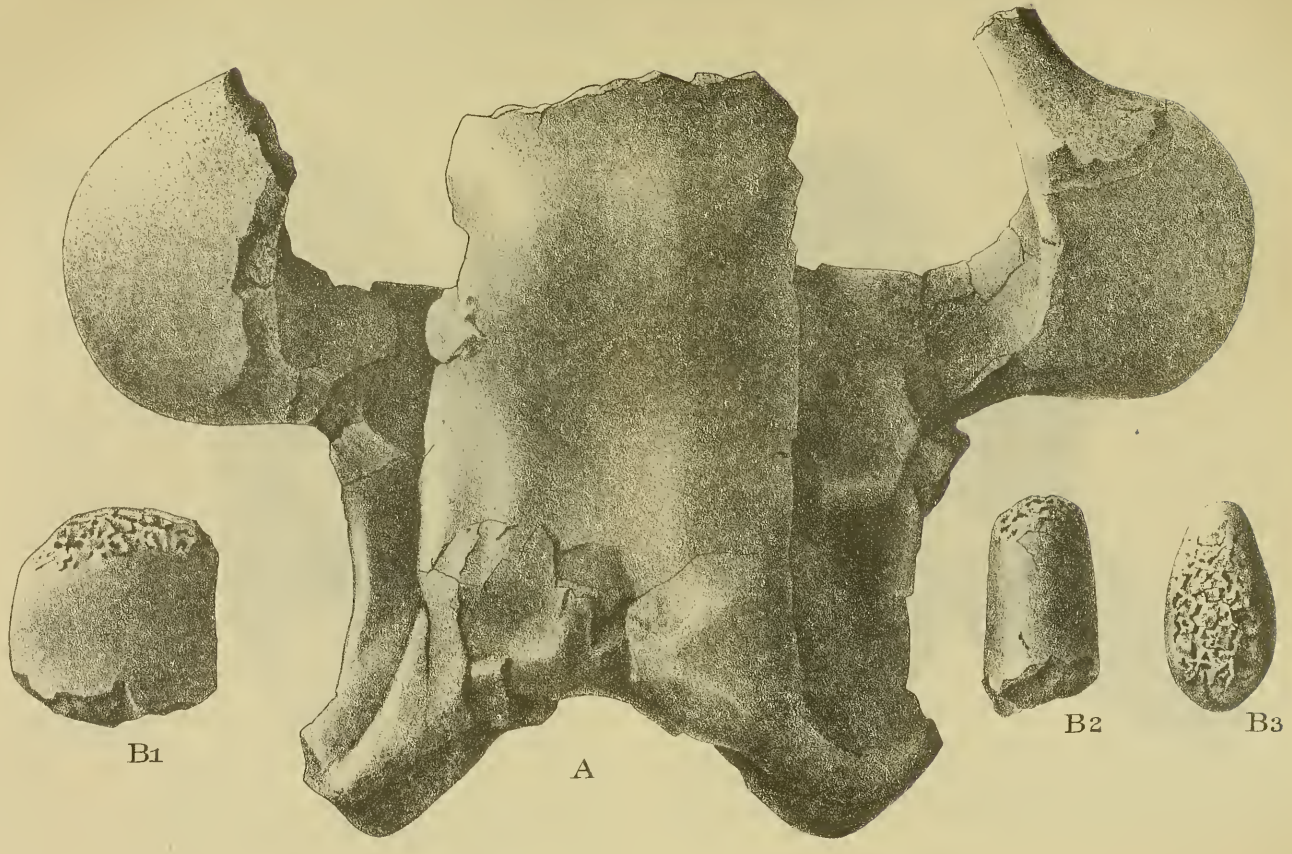
PLATE CLXXXIII

Skull of Brontotherium curtum and Horn of Brontotherium hypoceras

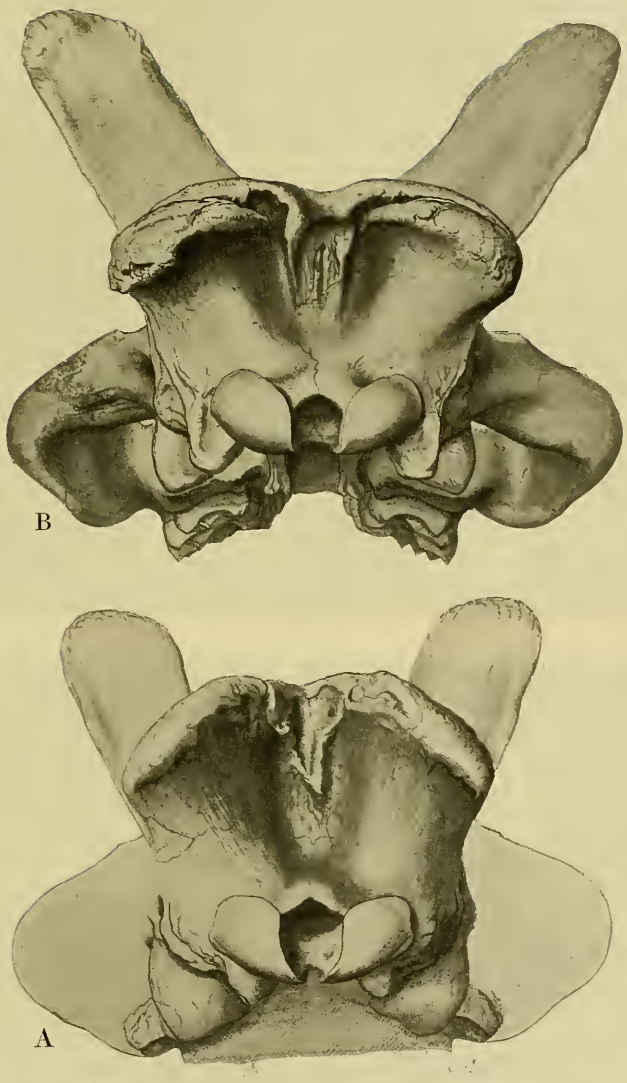
Plate prepared under the direction of Professor Cope. (See pp. 212, 562, also Pls. CLXVI and CLXXXV)

A, Skull referred to *Brontotherium curtum* (Am. Mus. 6346), cotype of *Symborodon bucco* Cope, Horsetail Creek, northeastern Colorado, Chadron formation. One-third natural size. This is one of the specimens upon which Cope founded his species *Symborodon bucco*, but it was not the leading specimen of the original description, and it appears to be generically distinct from the lectotype of that species. (See p. 212 and Pl. CLV.) The reference to *Brontotherium curtum* is based especially upon the similarity in the zygomatic arches and cranial vertex.

B_1, B_2, B_3, Fragment of horn, part of type of *Brontotherium hypoceras* (Cope) (Am. Mus. 6361), northeastern Colorado, Chadron formation. (Compare Pl. CLXVI.)



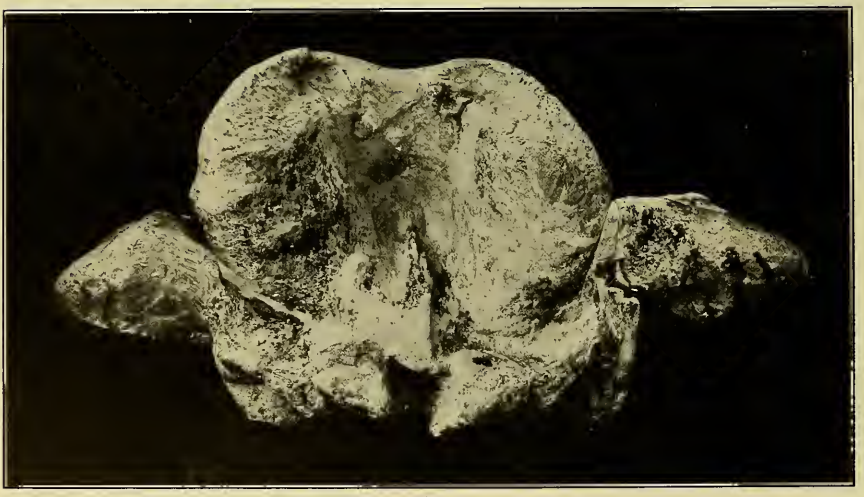
SKULL OF BRONTOTHERIUM CURTUM AND HORN OF B. HYPOCERAS



SKULLS OF BRONTOTHERIUM GIGAS AND B. CURTUM

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See pp. 568, 575, also Pls. CLXXV and CLXXIX.) A, Skull referred to *Brontotherium gigas*? (Yale Mus. 12061?), South Dakota, Chadron formation, probably upper levels. Occiput of type skull of *Titanops elatus* Marsh? As compared with B. *curtum*, the occiput is narrow and the depression for the ligamentum nuchae is less extensive. B, *Brontotherium curtum*, type (Yale Mus. 12013), Colorado, Chadron formation, upper beds (Hatcher). Occiput of type skull of *Titanops curtus* Marsh. The occiput is wider, with a deep insertion area for the ligamentum nuchae and widely flaring crests for the rectus capitis lateralis muscles

B



A

SKULLS OF BRONTOTHERIUM CURTUM

One-fifth natural size. (See p. 575, also Pls. CLXXVII and CLXXXIII.) A, Occiput referred to *Brontotherium curtum* (Am. Mus. 6346), Horsetail Creek, northeastern Colorado, Chadron formation. As remarked above (Pl. CLXXXIII), this specimen is one of the cotypes selected by Cope for his species of "*Symborodon bucco*." The insertion areas for the ligamentum nuchae and for the rectus capitis lateralis muscles are well shown. The skull is a little crushed downward. B, Front view of skull referred to *Brontotherium curtum*? (Nat. Mus. 4946), skull q, Big Badlands, S. Dak. (Indian Draw), Chadron formation, level upper C (Hatcher). This view shows well the elevation of the nasal region in uncrushed skulls. The right horn has been broken off during life. The infraorbital canals are subcircular, as in other brontotheres

PLATE CLXXXVI

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PLATE CLXXXVI

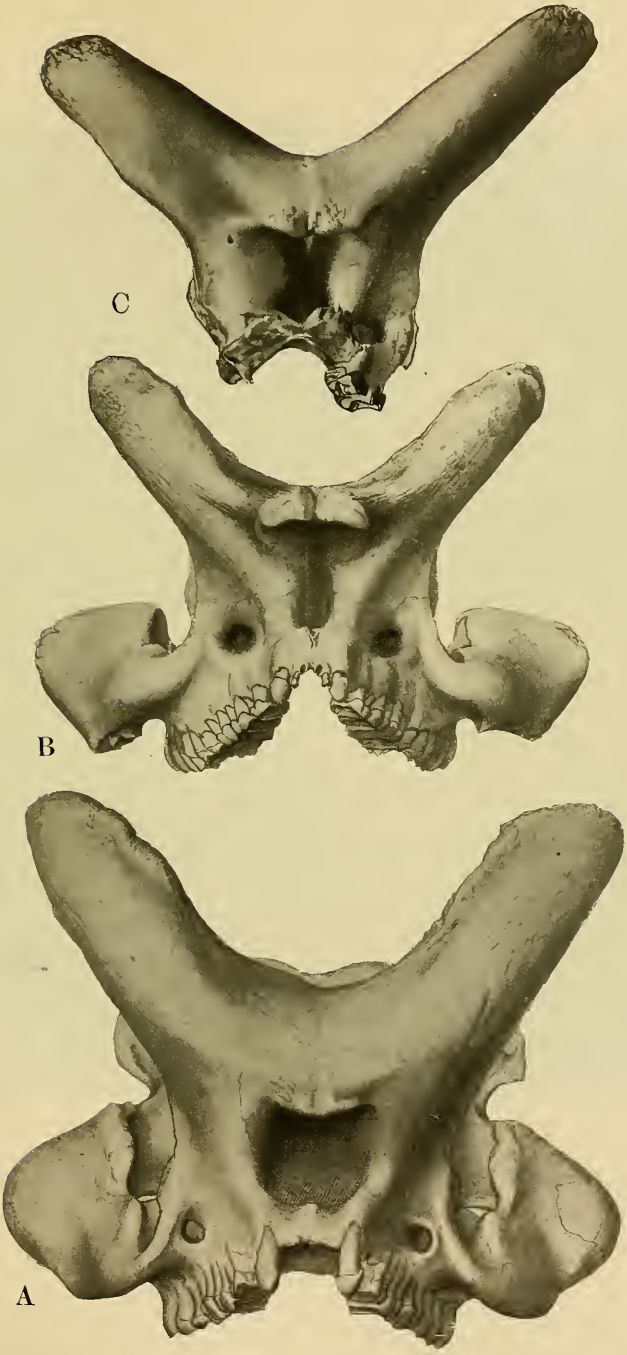
Skulls of Brontotherium and Megacerops

Plate prepared under the direction of Professor Marsh. One-sixth natural size. (See p. 575)

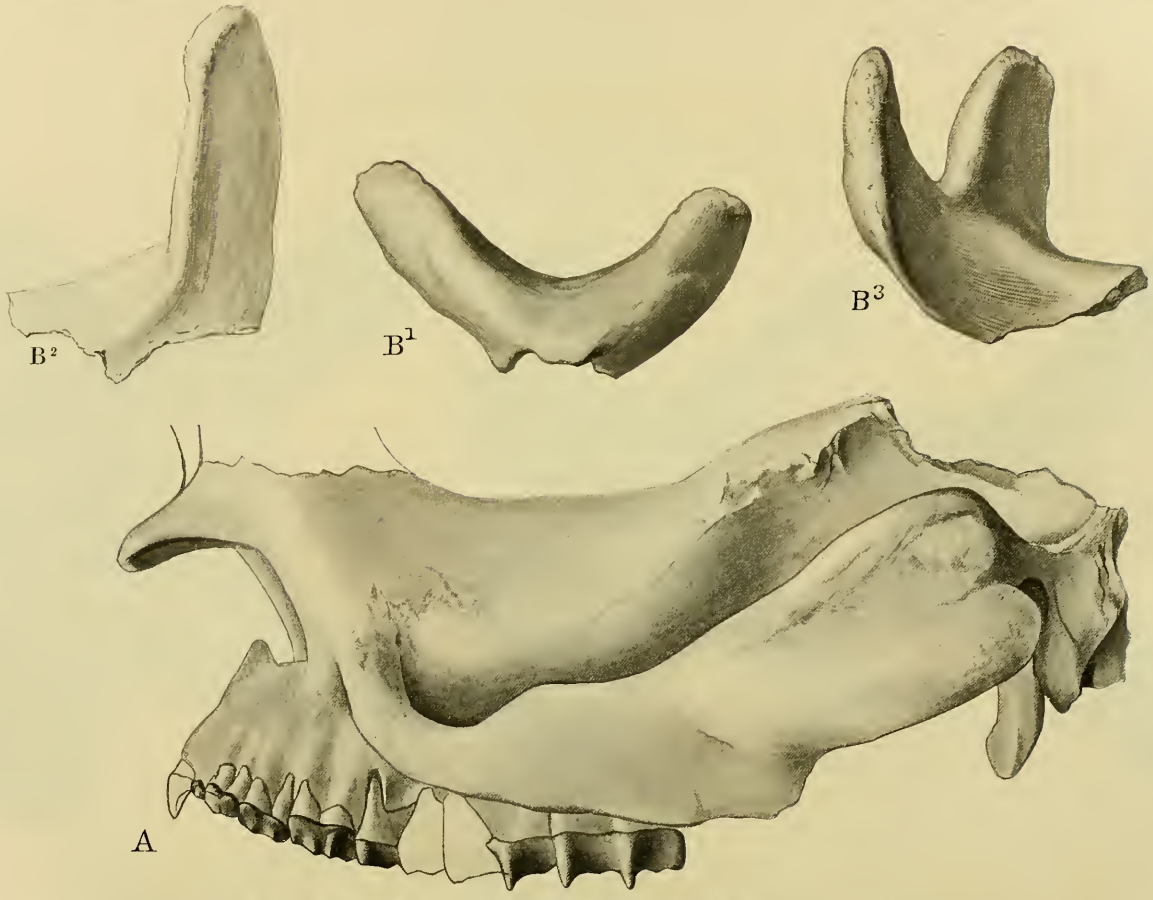
A, *Brontotherium curtum*, type (Yale Mus. 12013), Colorado, Chadron formation, upper levels. Front view. Type of *Titanops curtus* Marsh. The long horns in this highly specialized brontothere are much flattened in cross section and much larger than in the type of *B. platyceras*. The incisors are not preserved.

B, Skull referred to *Megacerops?* sp. (Nat. Mus. 1220?). This skull appears to be allied to *Megacerops torvus* or *M. acer*. As in that genus, the nasals are short and thick, the horns elongate, slender, the zygomata massive and thick vertically. The presence of two incisors does not definitely exclude this specimen from *Megacerops*, because the type of *M. acer* retains alveoli for two small incisors.

C, Type skull of *Brontotherium dolichoceras* (Harvard Mus.), South Dakota, Chadron formation. In this specimen the horns are more slender and less widened transversely than in other brontotheres. They are suboval at the base. In *Megacerops* a connecting crest is usually lacking and the horns are thicker at the base.



SKULLS OF BRONTOTHERIUM AND MEGACEROPS



SKULL OF MALE BRONTOTHERIUM TICHOCERAS AND HORNS OF B. PLATYCERAS

(See pp. 567, 579.) A, Type skull of *Brontotherium* ("*Menodus*") *tichoceras* (Harvard Mus.), South Dakota, Chadron formation. One-fourth natural size. In the relative length of the nasals, the great thickness of the base of the horns, and the dimensions of the skull and grinding series this specimen finds its nearest allies in *B. hatcheri* and *B. gigas*. B¹, Type horns of *Brontotherium* ("*Menodus*") *platyceras* (Harvard Mus.), South Dakota, Chadron formation. One-sixth natural size. Front view of horns and nasals, the latter broken at the tip. These type horns are distinguished by the convex-concave section. They are much smaller than those of *B. curtum*. They are about as large as those in *B. hatcheri* but much flatter. B², The same, side view. Scale unknown, possibly one-fifth natural size. B³, The same, postero-external view, showing the flatness of the horns and the high connecting crest

SKULL OF MALE BRONTOTHERIUM PLATYCERAS

One-fifth natural size. (See p. 579, also Pl. CLXXXIX.) Skull referred to *Brontotherium platyceras* (Am. Mus. 1448), Cheyenne River badlands, S. Dak., Chadron formation. This brontothere has the longest recorded horns and the shortest recorded nasals. The horns in size resemble those of *B. curtum* and are far larger than those of the type of *B. platyceras*. The width of the zygomata has been increased by vertical crushing, which has also lessened the height of the anterior narial opening and caused the horns to pitch sharply forward. The jaw here shown (Am. Mus. 1051) may belong to some other species

PLATE CLXXXIX

PLATE CLXXXIX

Skull of Brontotherium platyceras

One-fifth natural size. (See p. 579, also Pl. CLXXXVIII)

Skull referred to *Brontotherium platyceras* (Am. Mus. 1448), Cheyenne River Badlands, S. Dak., Chadron formation, probably from the upper part of the *Titanotherium* zone. This side view shows the extreme length of the horns and height of the connecting crest in this brontothere. Vertical crushing has pitched the horns forward, so that the nasals are now far in advance of the skull. The zygomata also are displaced forward. The jaw (Am. Mus. 1061) does not belong with the skull. The relationship of this animal to *B. platyceras* and *B. curtum* is discussed above. (See Pl. CLXXXVIII.)

SKULL OF BRONTOTHERIUM PLATYCERAS

PLATE CXC

PLATE CXC

Skulls of Female Brontotherium

(See pp. 571, 576, also Pl. CXCII)

A, Female skull referred to *Brontotherium? gigas?* (Am. Mus. 1006), Big Badlands, S. Dak., Chadron formation. One-fifth natural size. This specimen was referred to the genus and species *B. gigas* on account of the similarity of the basal section of the horns, but the characters of the canines and premolars suggest reference to *Brontops* cf. *B. robustus.*

B^1, B^2, Female skull referred to *Brontotherium curtum* (Am. Mus. 1005), Big Badlands, S. Dak., Chadron formation. One-fifth natural size. This specimen is undoubtedly a brontothere, as shown especially by its premolars. The short horns are very massive at the base, and the connecting crest is high. Somewhat similar horns were described by Cope under the name *Menodus peltoceras.* (See p. 229.)

B 2

B 1

A

SKULLS OF FEMALE BRONTOTHERIUM

PLATE CXCI

PLATE CXCI

Skull of Male Brontotherium ramosum

One-sixth natural size. (See p. 577)

Am. Mus. 1447, type, Quinn Draw, Big Badlands, S. Dak., Chadron formation, upper levels. A_1, Side view; A_2, front view. The specific name refers to the branching character of the horn tips. The horns are extremely broad, resembling those of the Field Museum specimen shown in Plate CLXXXI. Vertical crushing has flattened the skull and zygomata. The lower jaw (Am. Mus. 1062; Cheyenne River badlands, S. Dak., Chadron formation) does not belong with this skull.

A ²

A ¹

SKULL OF MALE BRONTOTHERIUM RAMOSUM

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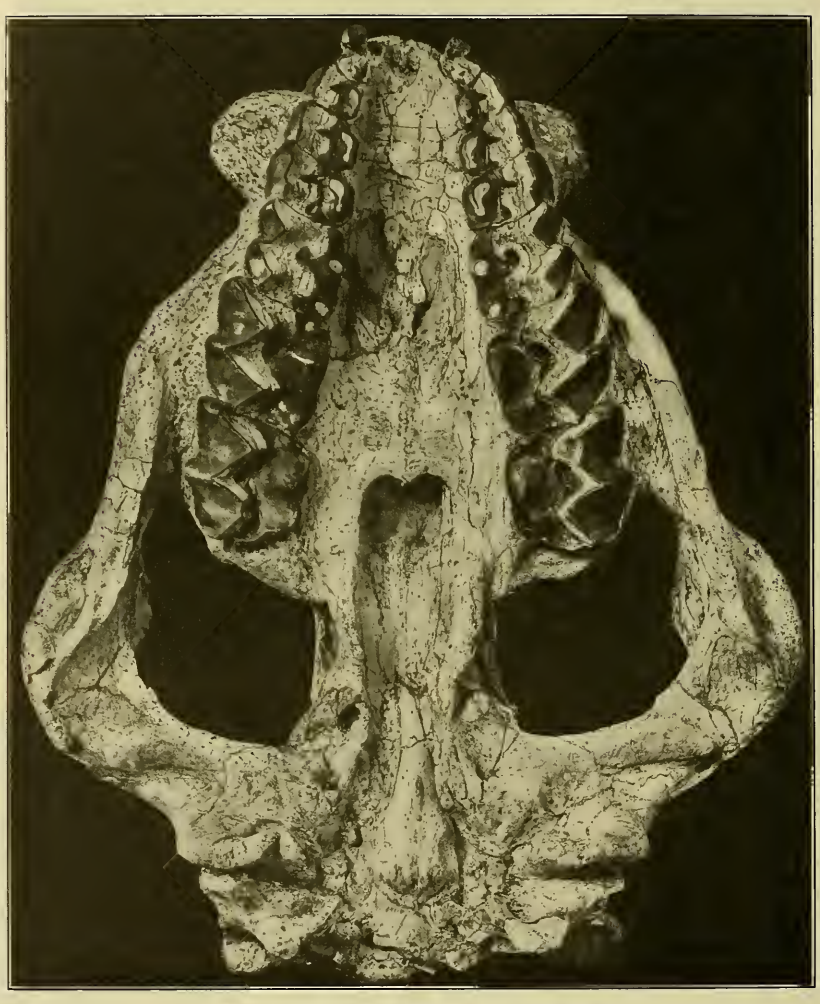


SKULL OF FEMALE BRONTOTHERIUM CURTUM

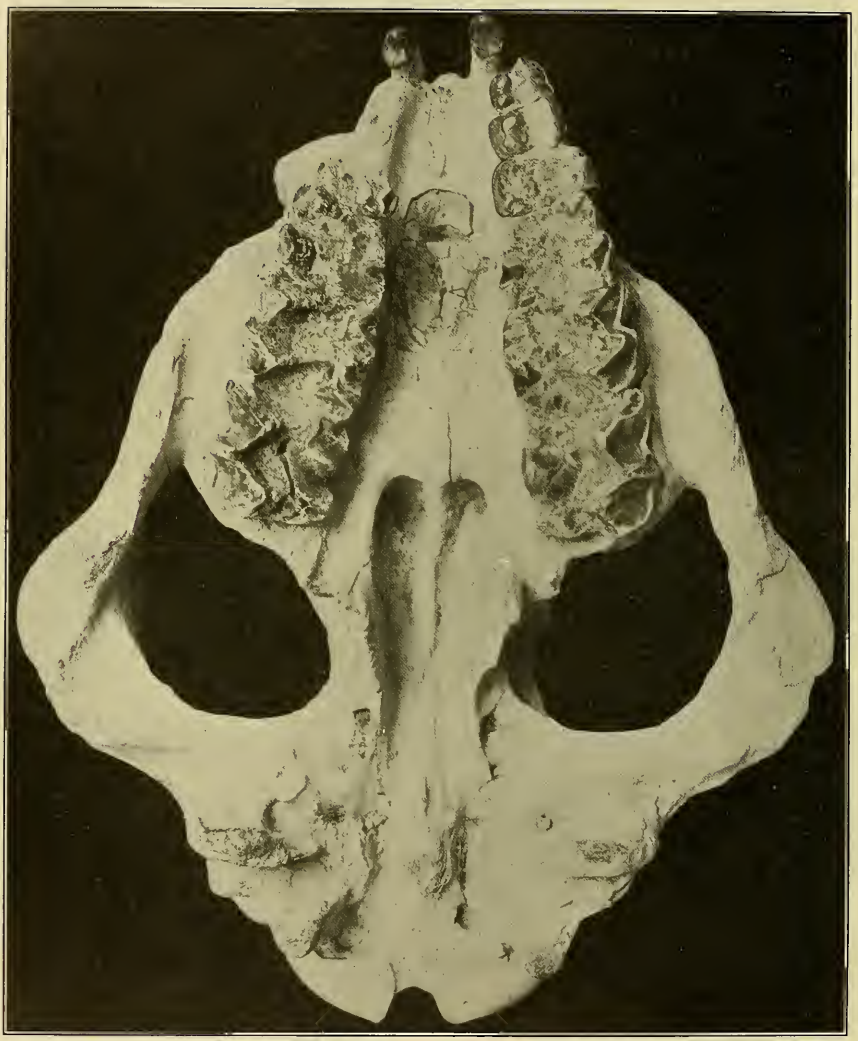
One-fourth natural size. (See p. 576, also Pl. CXC.) Referred skull (Am. Mus. 1005), Big Badlands, S. Dak., Chadron formation. The premolars and molars show the characters typical of *Brontotherium*, save that the postero-internal cusps of the premolars are not well separated from the antero-internal cusps. The canines are slender. The zygomata, though stout, are less expanded than in long-horned males

A²

A¹

SKULL OF FEMALE BRONTOTHERIUM CURTUM

One-fifth natural size. (See p. 577, also Pl. CXCIV.) Referred skull (British Mus. 5629). A¹, Top view; A², front view. This specimen so strongly resembles Cope's fragmentary type of *Menodus peltoceras* that it might be selected as a neotype. Kinship with the supposed female of *B. curtum* (Pl. CXCII) is indicated especially in the horns, nasals, zygomata, and dentition; but the canines seem too large to belong to a female, so that possibly this and the supposed female together with Cope's type may represent a distinct species of *Brontotherium*



SKULL OF FEMALE BRONTOTHERIUM CURTUM

One-fourth natural size. (See p. 577, also Pl. CXCIII.) British Mus. 5629. This palatal view shows well the long canines and the premolar characters, which are similar to those of the specimen figured in Plate CXCII

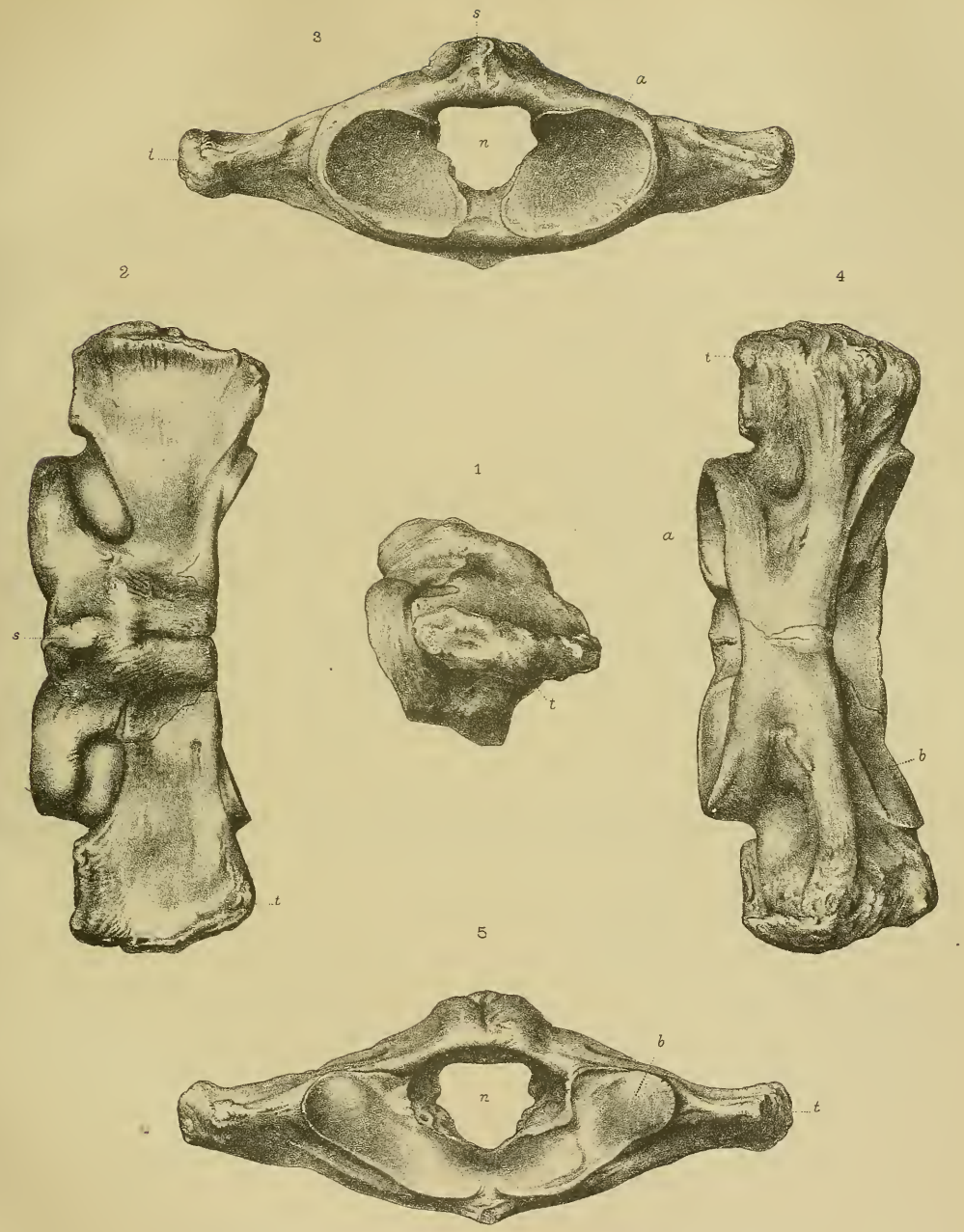
PLATE CXCV

PLATE CXCV

Atlas of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

Type (Yale Mus. 12048). 1, Lateral view, left side; 2, superior view; 3, anterior view; 4, inferior view; 5, posterior view. *a*, Facet for condyle of skull; *b*, facet for axis; *n*, neural canal; *s*, neural spine; *t*, transverse process.



ATLAS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

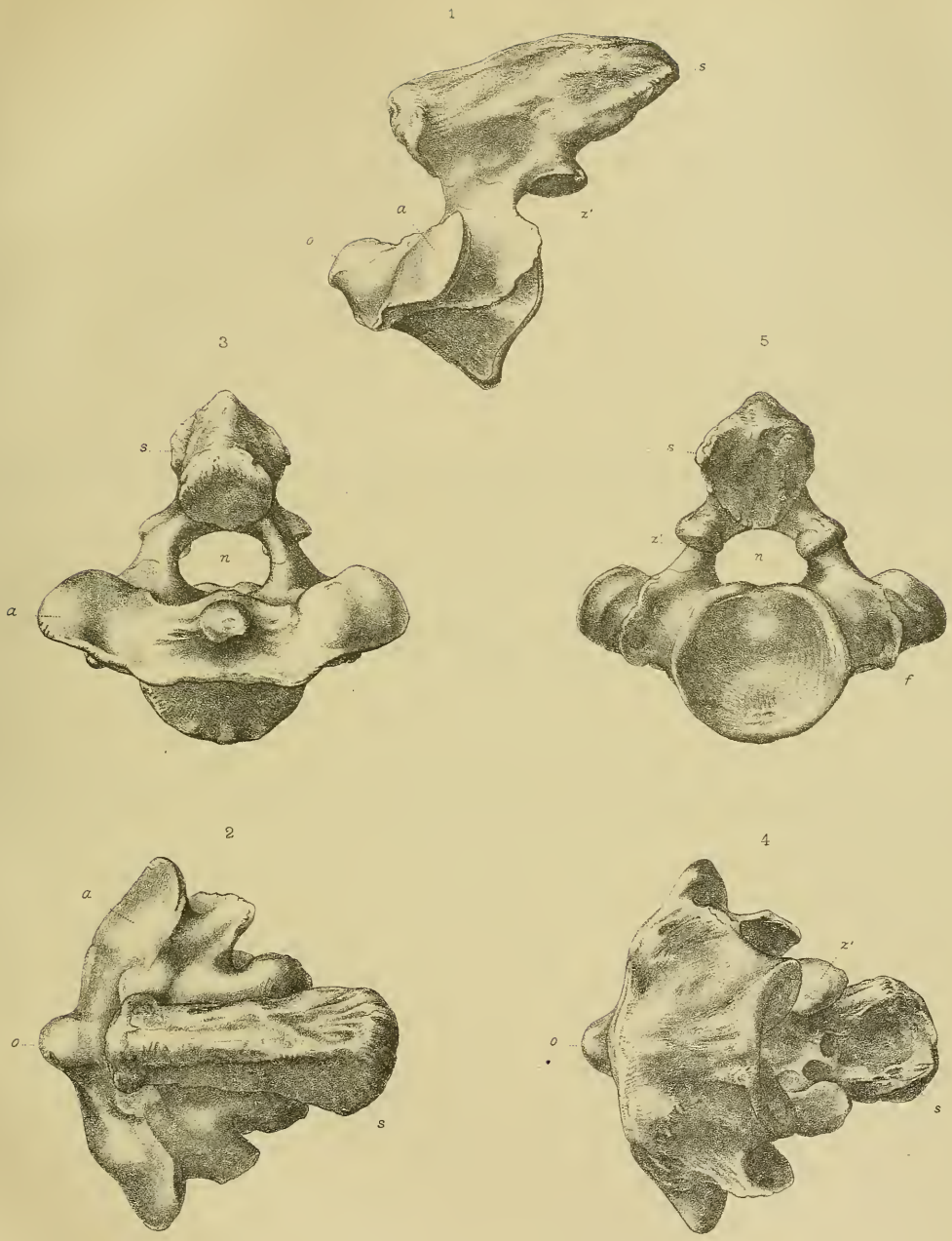
PLATE CXCVI

PLATE CXCVI

Axis of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One fourth natural size. (See p. 667)

1, Lateral view, left side; 2, superior view; 3, anterior view; 4, inferior view; 5, posterior view. *a*, Facet for atlas; *f*, foramen for vertebral artery; *n*, neural canal; *o*, odontoid process; *z'*, postzygapophysis. The principal muscle and ligament attachments of this vertebra are given on page 713.



AXIS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

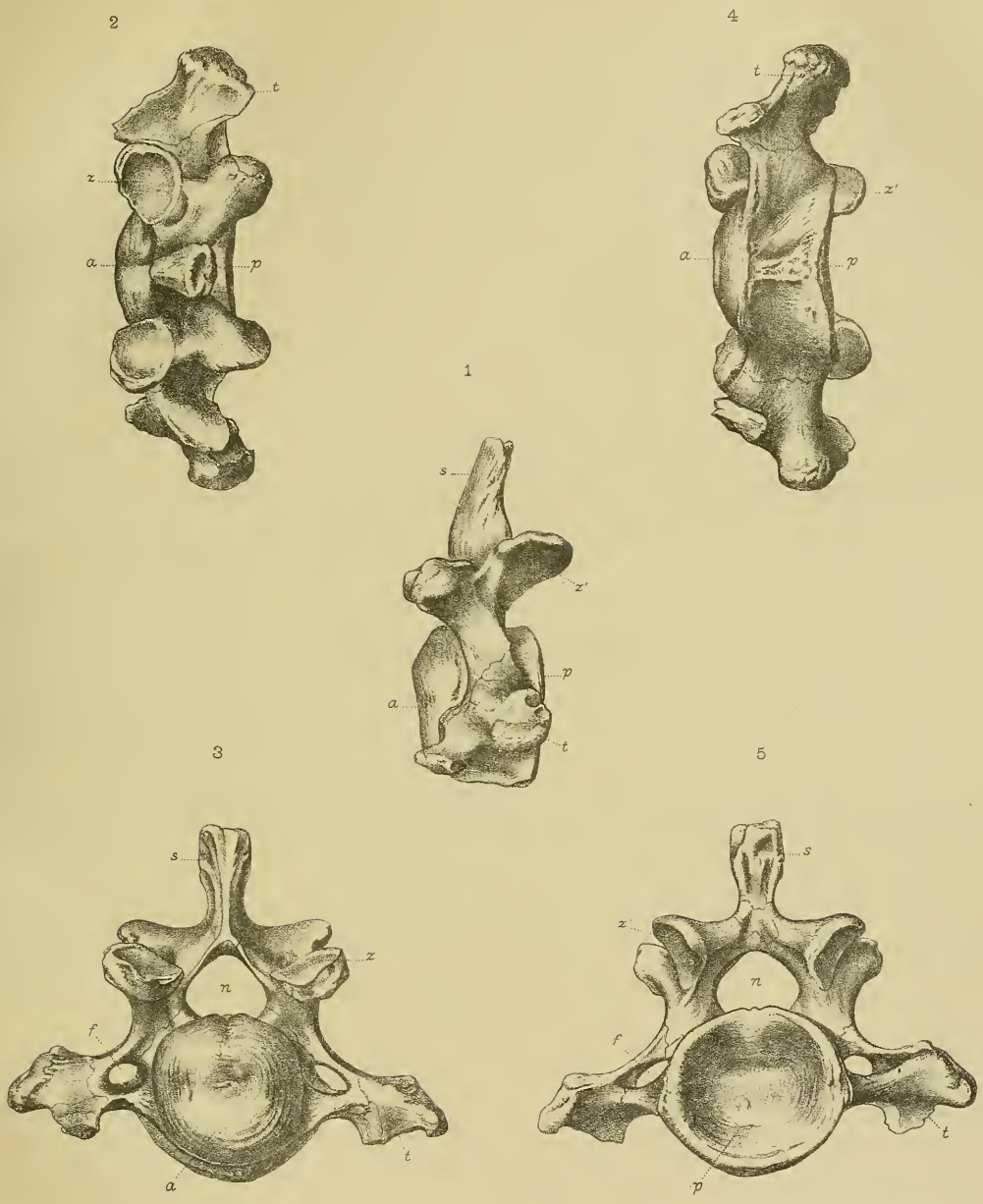
PLATE CXCVII

PLATE CXCVII

Fourth Cervical Vertebra of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, Lateral view, left side; 2, superior view; 3, anterior view; 4, inferior view; 5, posterior view. *a*, Anterior facet of centrum; *f*, foramen for vertebral artery; *n*, neural canal; *s*, neural spine; *t*, transverse process; *z*, prezygapophysis; *z'*, postzygapophysis. The principal muscle and ligament attachments of this vertebra are given on page 713.



FOURTH CERVICAL VERTEBRA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

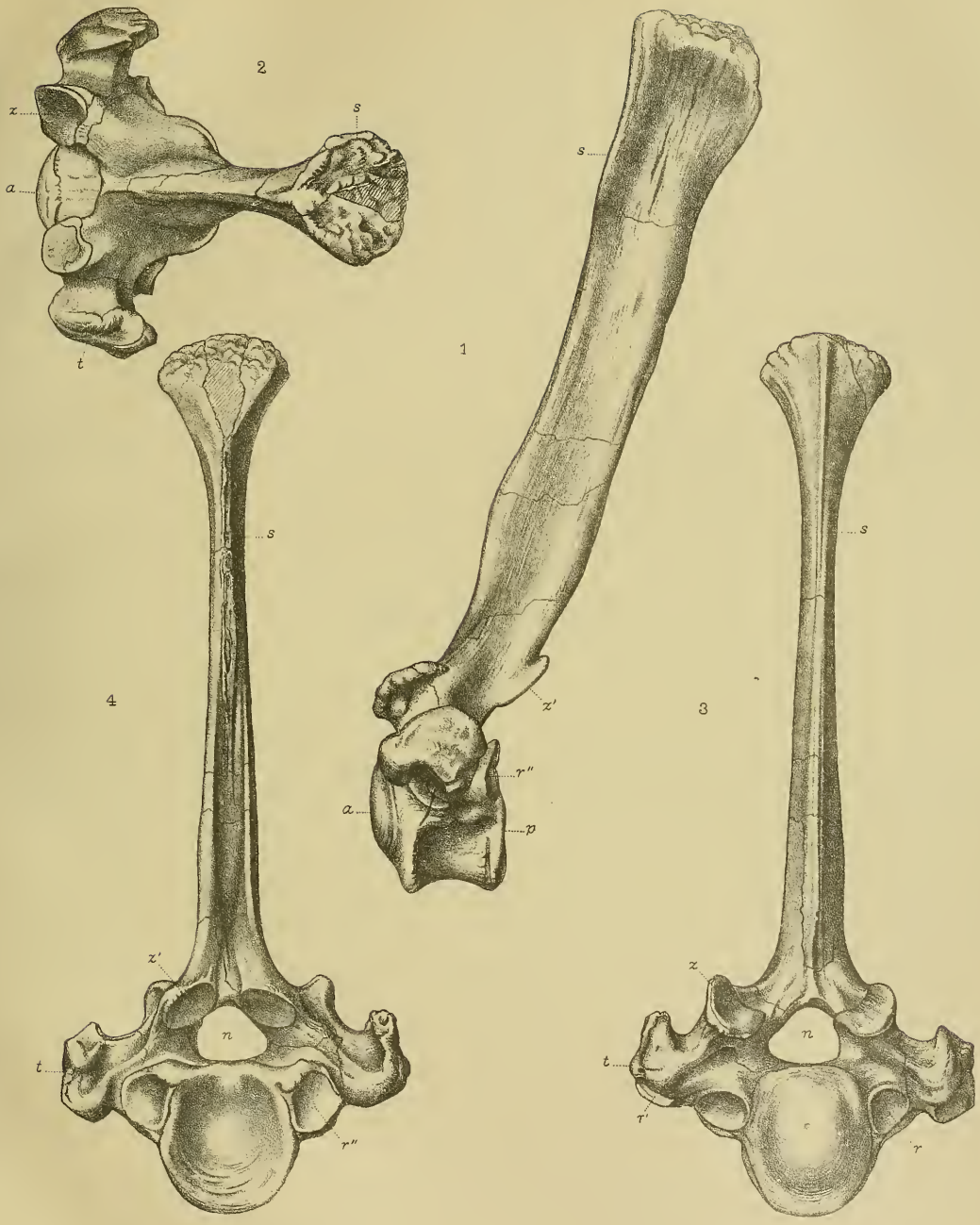
PLATE CXCVIII

PLATE CXCVIII

Second Dorsal Vertebra of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, Lateral view, left side; 2, superior view; 3, anterior view; 4, posterior view. *a*, Anterior facet of centrum; *n*, neural canal; *p*, posterior facet of centrum; *r*, facet for capitulum of second rib; *r'*, facet for tuberculum of second rib; *r''*, facet for capitulum of third rib; *t*, transverse process; *z*, prezygapophysis; *z'*, postzygapophysis. The principal muscle and ligament attachments of this vertebra are given on page 713.



SECOND DORSAL VERTEBRA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

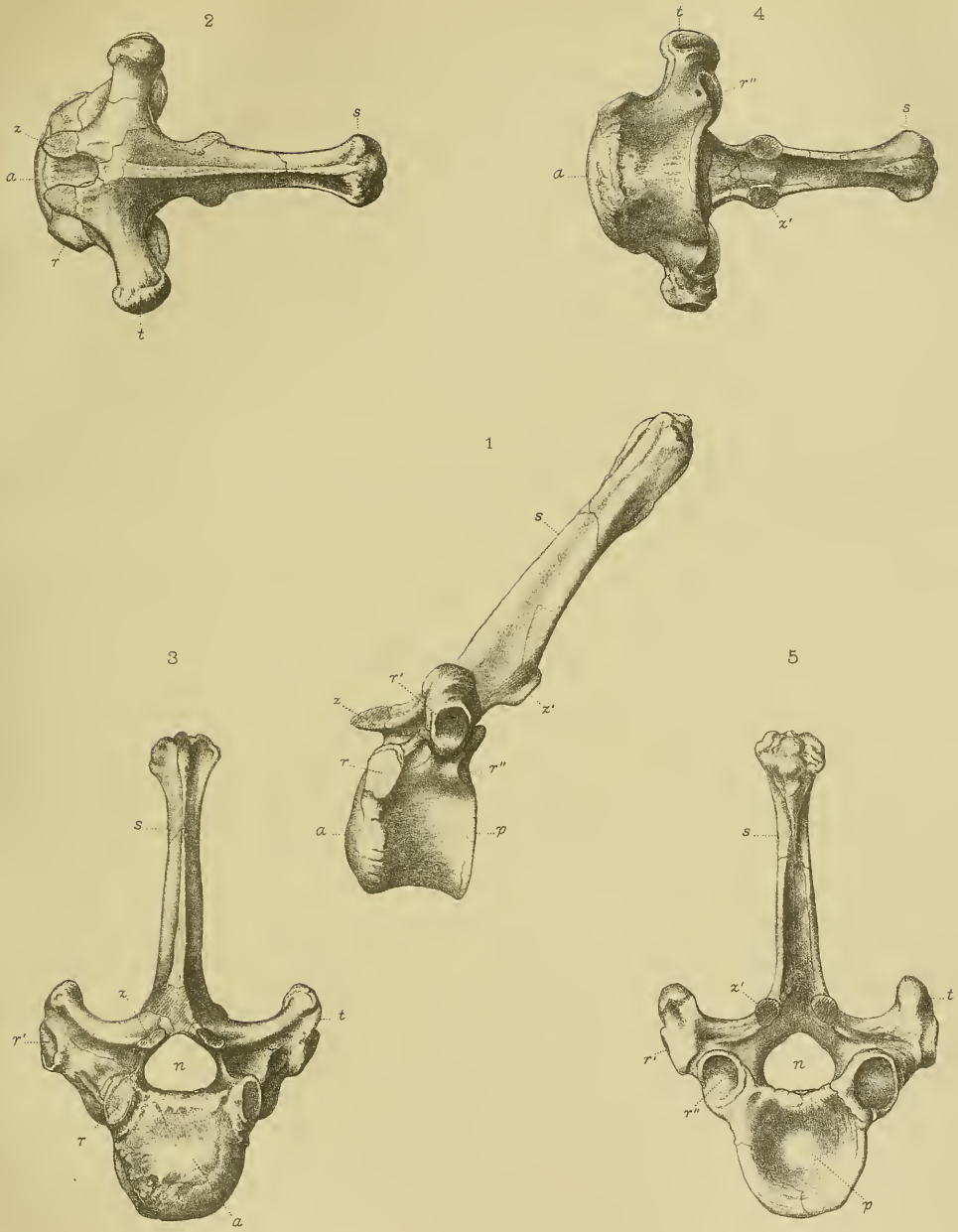
PLATE CXCIX

PLATE CXCIX

Tenth Dorsal Vertebra of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, Lateral view, left side; 2, superior view; 3, anterior view; 4, inferior view; 5, posterior view. *a*, Anterior facet of centrum; *n*, neural canal; *p*, posterior facet of centrum; *r*, facet for capitulum of tenth rib; *r'*, facet for tuberculum of tenth rib; *r''*, facet for capitulum of eleventh rib; *s*, neural spine; *t*, transverse process; *z*, prezygapophysis; *z'*, postzygapophysis.



TENTH DORSAL VERTEBRA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CC

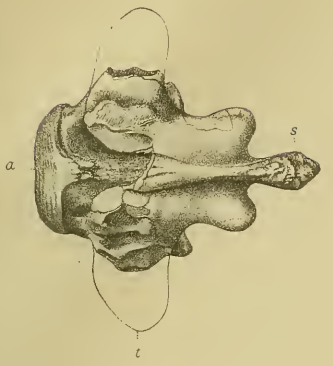
PLATE CC

Second Lumbar Vertebra of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, Lateral view, left side; 2, superior view; 3, anterior view; 4, inferior view; 5, posterior view. *a*, Anterior facet of centrum; *n*, neural canal; *p*, posterior facet of centrum; *s*, neural spine; *t*, transverse process; *z*, prezygapophysis; *z'*, postzygapophysis. The chief muscle and ligament attachments of this vertebra are given on page 713.

2



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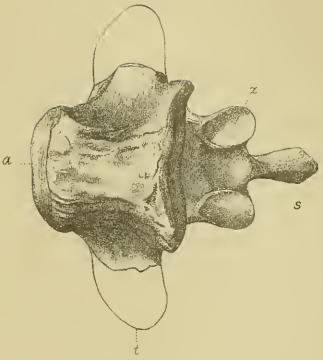

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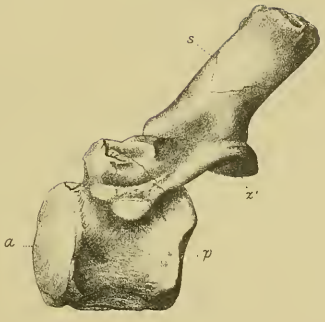

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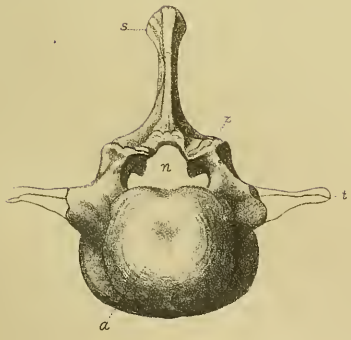

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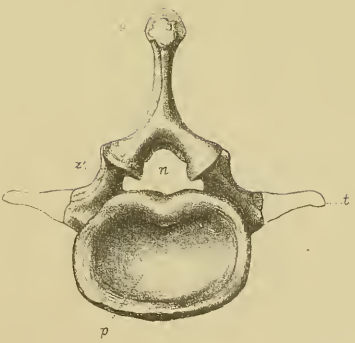

SECOND LUMBAR VERTEBRA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCI

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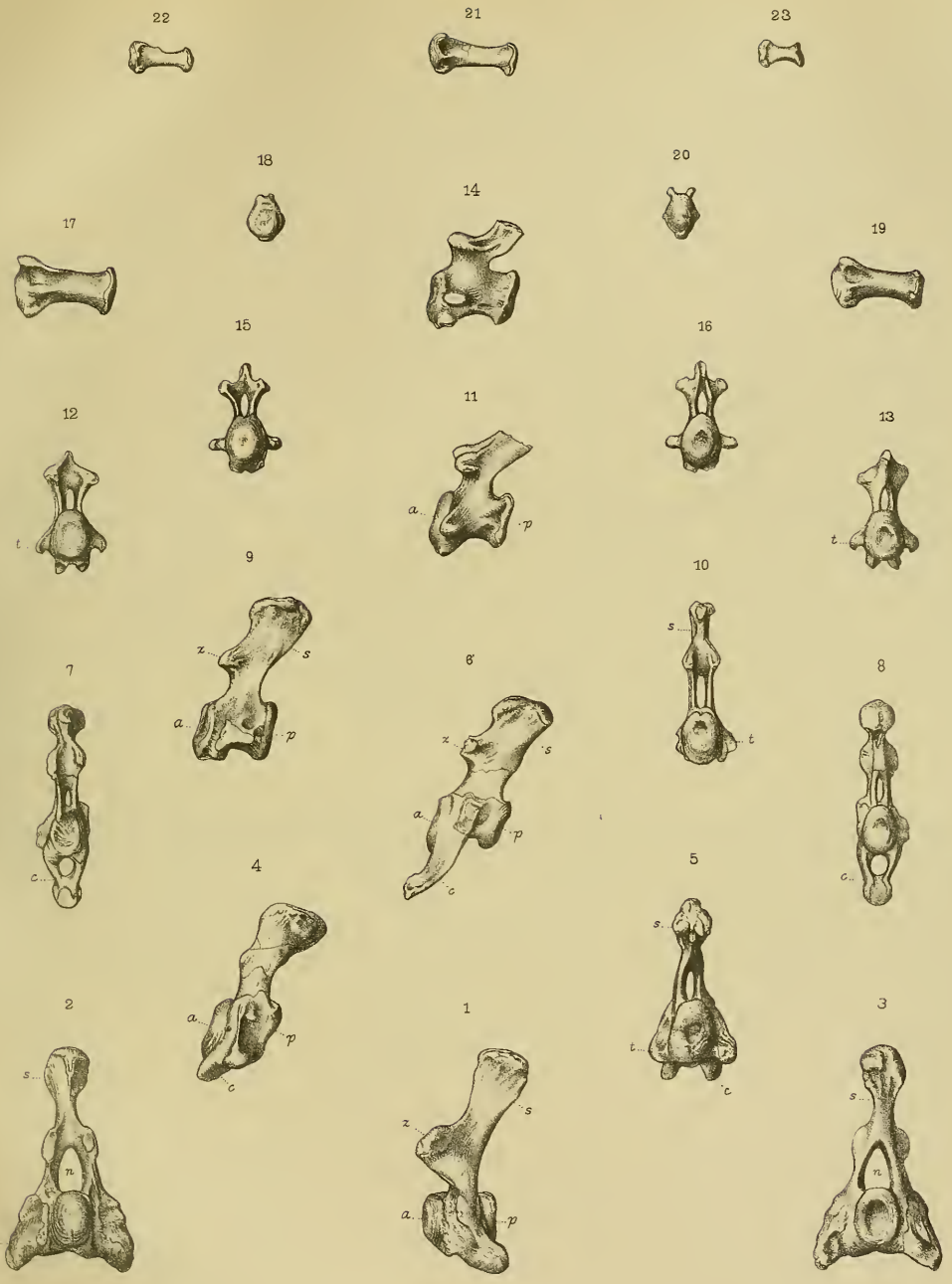
PLATE CCI

Caudal Vertebrae of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, First caudal, lateral view, left side; 2, the same, anterior view; 3, the same, posterior view; 4, second caudal, lateral view, left side; 5, second caudal, posterior view; 6, third caudal, lateral view, left side; 7, the same, anterior view; 8, the same, posterior view; 9, fourth caudal, lateral view, left side; 10, the same, anterior view; 11, fifth(?) caudal, lateral view, left side; 12, the same, anterior view; 13, the same, posterior view; 14, seventh(?) caudal, lateral view, left side; 15, the same, anterior view; 16, the same, posterior view; 17, tenth(?) caudal, lateral view, left side; 18, the same, anterior view; 19, twelfth(?) caudal, lateral view, left side; 20, the same, anterior view; 21, thirteenth(?) caudal, lateral view, left side; 22, fifteenth(?) caudal, lateral view, left side; 23, sixteenth(?) caudal, lateral view, left side. *a*, Anterior; *c*, hemapophysis; *n*, neural canal; *p*, posterior; *s*, neural spine; *t*, transverse process; *z*, prezygapophysis.



CAUDAL VERTEBRAE OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

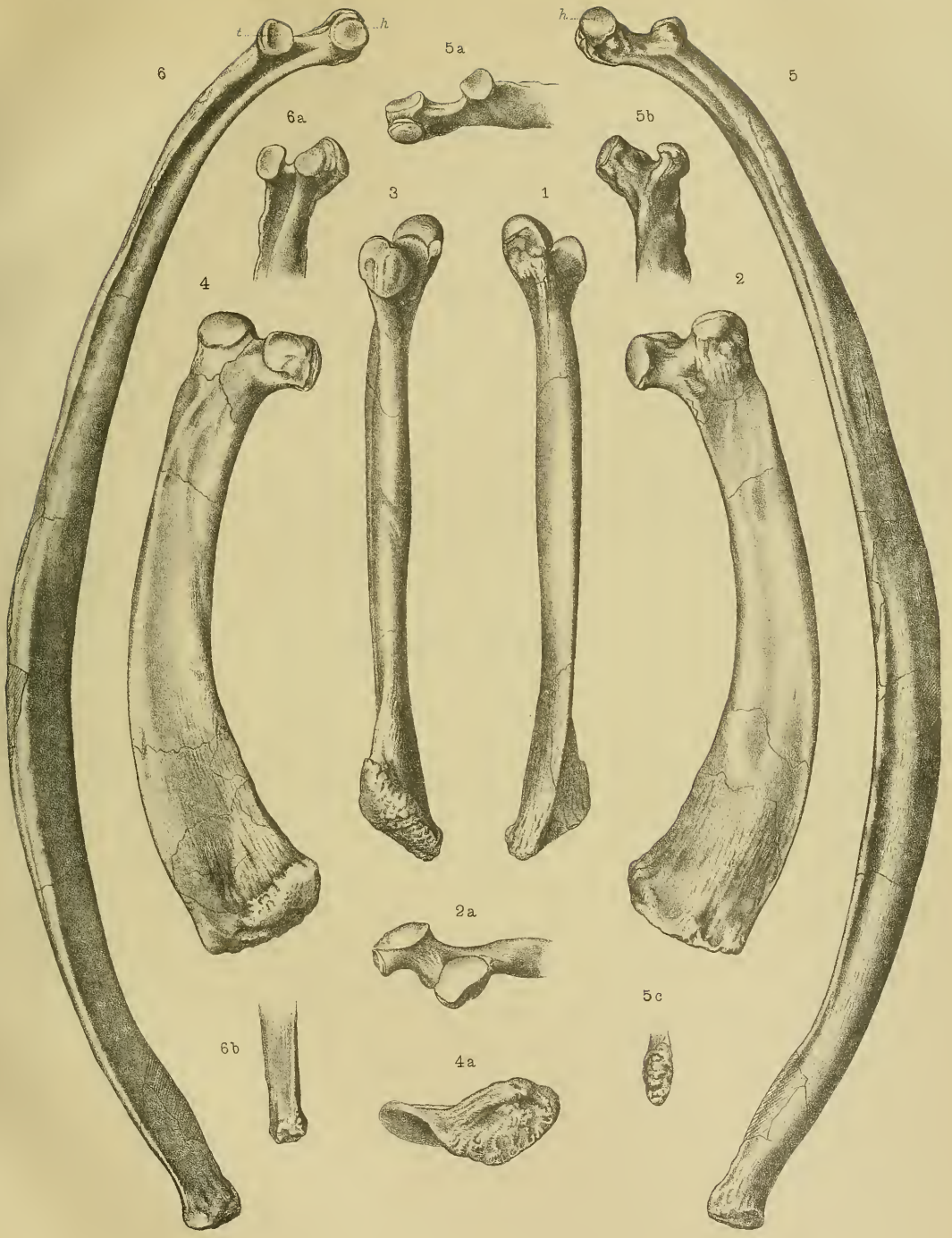
PLATE CCII

PLATE CCII

Second and Tenth Left Ribs of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, Second rib, outer view; 2, the same, anterior; 2a, the same, proximal end; 3, the same, inner view; 4, the same, posterior view; 4a, the same, distal view; 5, tenth rib, anterior view; 5a, the same, proximal end, dorsal view; 5b, the same, proximal end, antero-internal view; 5c, the same, distal view; 6, the same, posterior view; 6a, the same, internal view; 6b, the same, distal end, internal view.



SECOND AND TENTH LEFT RIBS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

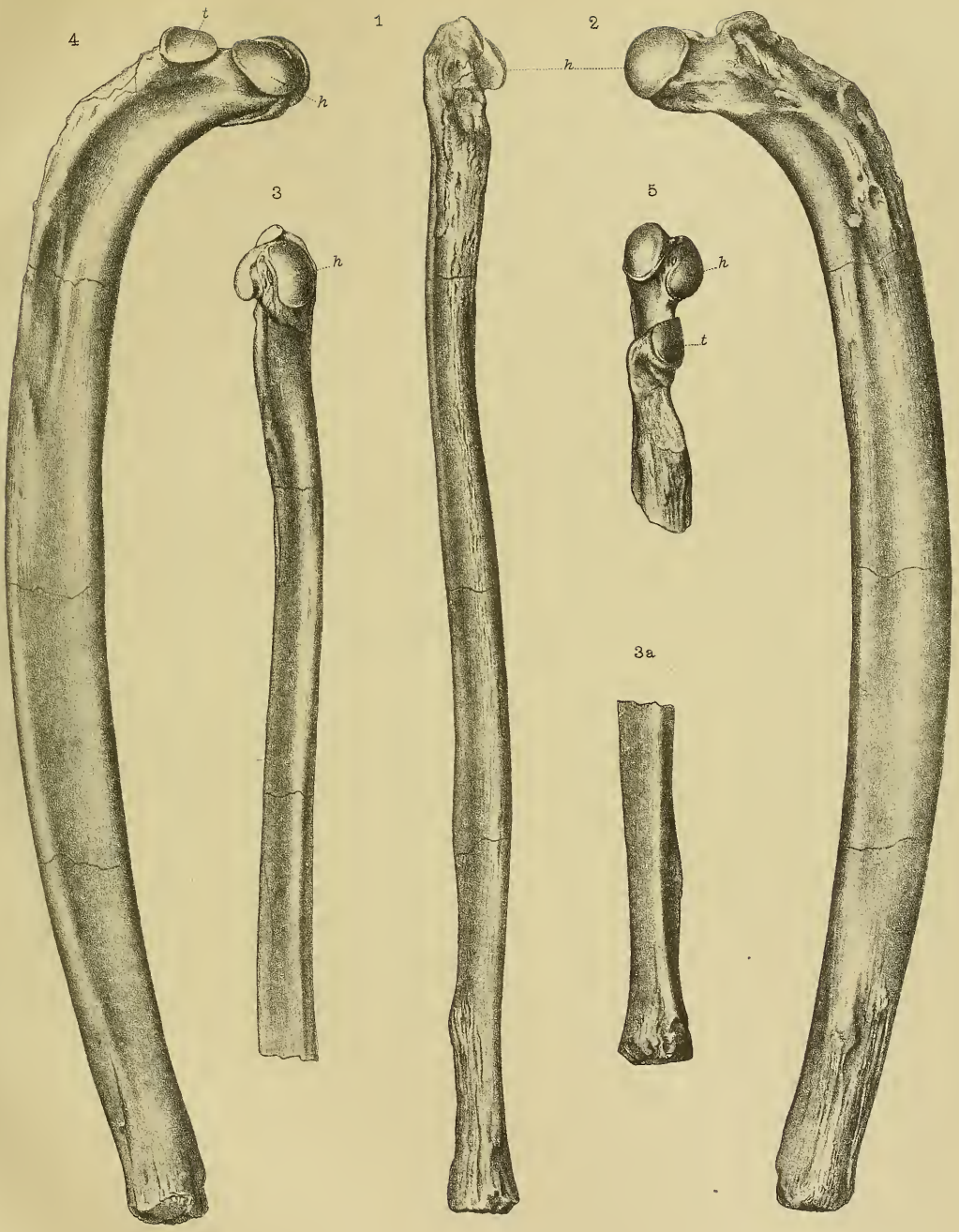
PLATE CCIII

PLATE CCIII

Fourth Rib of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 667)

1, Outer view; 2, anterior view; 3, inner view; 3a, inner view; 4, posterior view; 5, superior view of upper portion. *h*, Head of rib; *t*, tubercle of rib.



FOURTH RIB OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

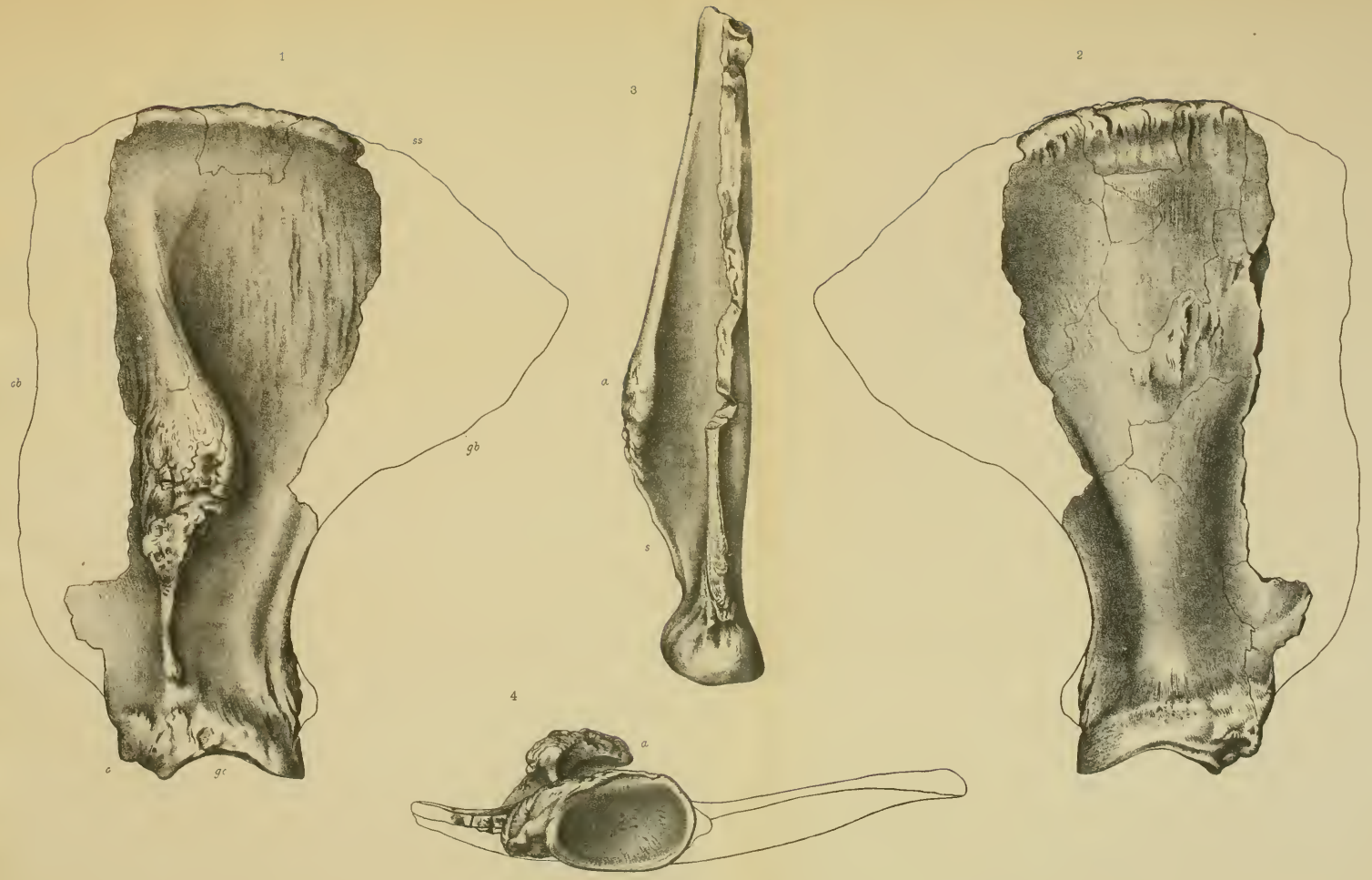
PLATE CCIV

PLATE CCIV

Left Scapula of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 668)

1, Lateral or external view, left side; 2, medial or inner view; 3, posterior view; 4, inferior or distal view. *a*, Tuberosity for the trapezius muscle, running below into a ridge for the acromial portion of the deltoid; *c*, coracoid process with rugosity for the biceps and coracobrachialis muscle; *cb*, cervical or anterior border of the scapula, ending below in a tuberosity which was probably the origin of the caput longum tricipitis and infraspinatus secundus muscles; *s*, spine of the scapula; *ss*, suprascapular border with rugosity for insertion of the rhomboideus muscle. The principal muscle attachments of the scapula are given on page 714.



LEFT SCAPULA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

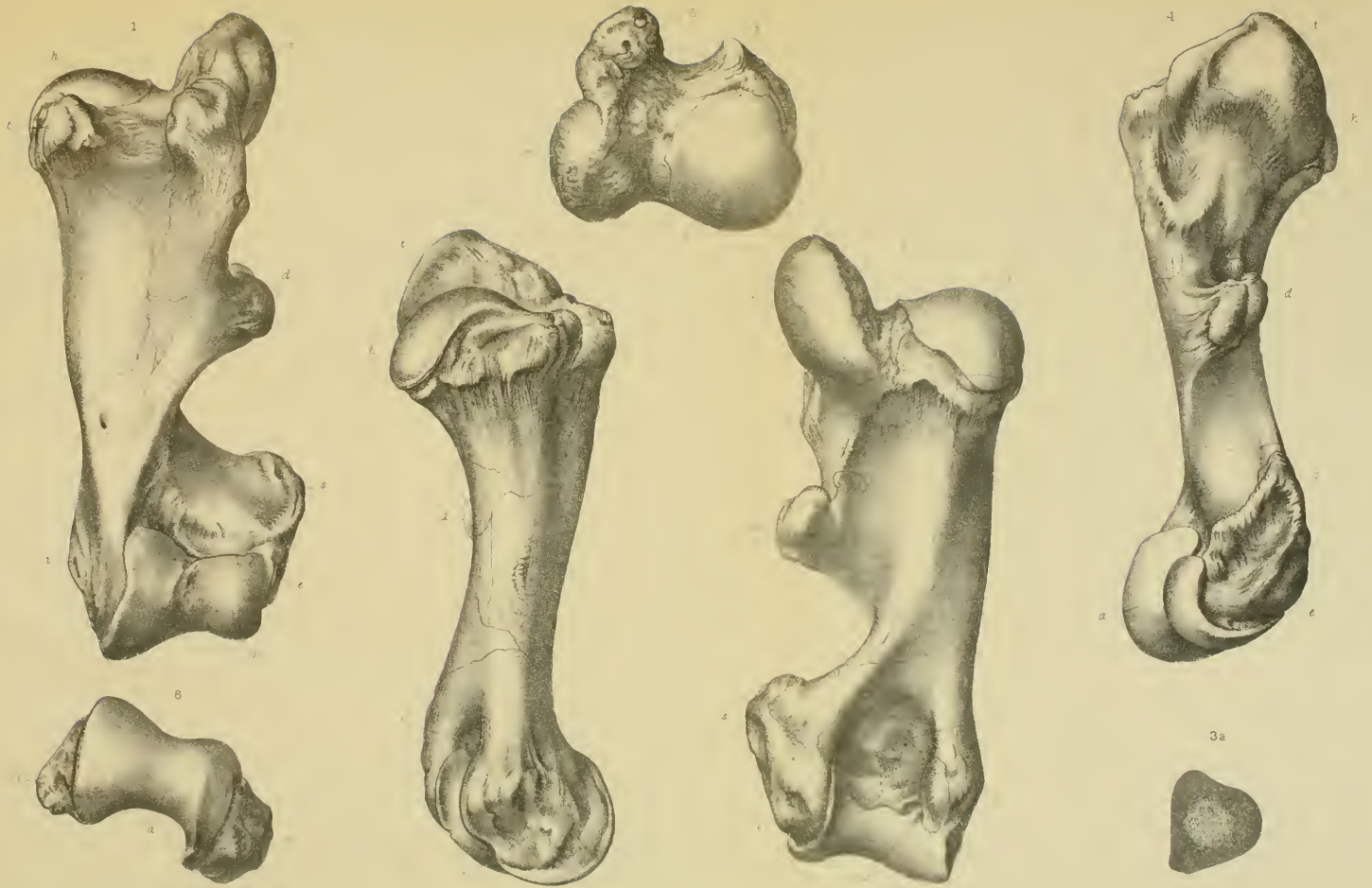
PLATE CCV

PLATE CCV

Left Humerus of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 668)

1, Anterior view; 2, medial or inner view; 3, posterior view; 3a, section of shaft at narrowest point; 4, lateral or outer view; 5, proximal end; 6, distal end. *a*, Distal articular surface; *d*, deltoid ridge; *e*, external condyle; *h*, head of humerus; *i*, internal condyle; *o*, anconeal fossa; *s*, supinator ridge; *t*, great tuberosity; *t'*, small tuberosity. The principal muscle attachments of the humerus are given on page 715.



LEFT HUMERUS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

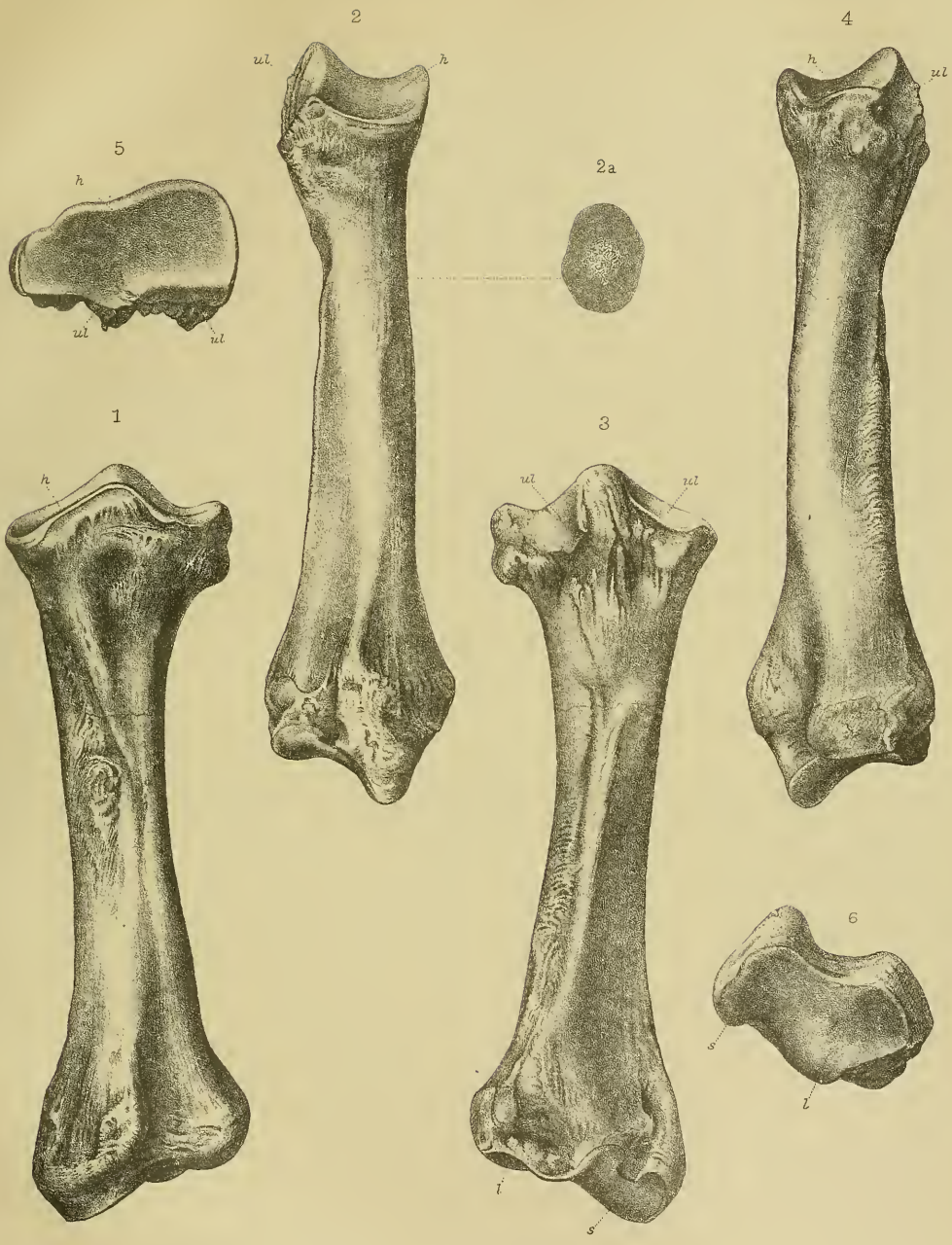
PLATE CCVI

PLATE CCVI

Left Radius of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 668)

1, Anterior view; 2, medial or inner view; 2a, section of shaft at point indicated by dotted line; 3, posterior view; 4, lateral or outer view; 5, proximal end; 6, distal end. *h*, Articular facet for humerus; *l*, articular facet for lunar; *s*, articular facet for scaphoid; *ul*, articular facet for ulna. The principal muscle attachments of the radius are given on page 716.



LEFT RADIUS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

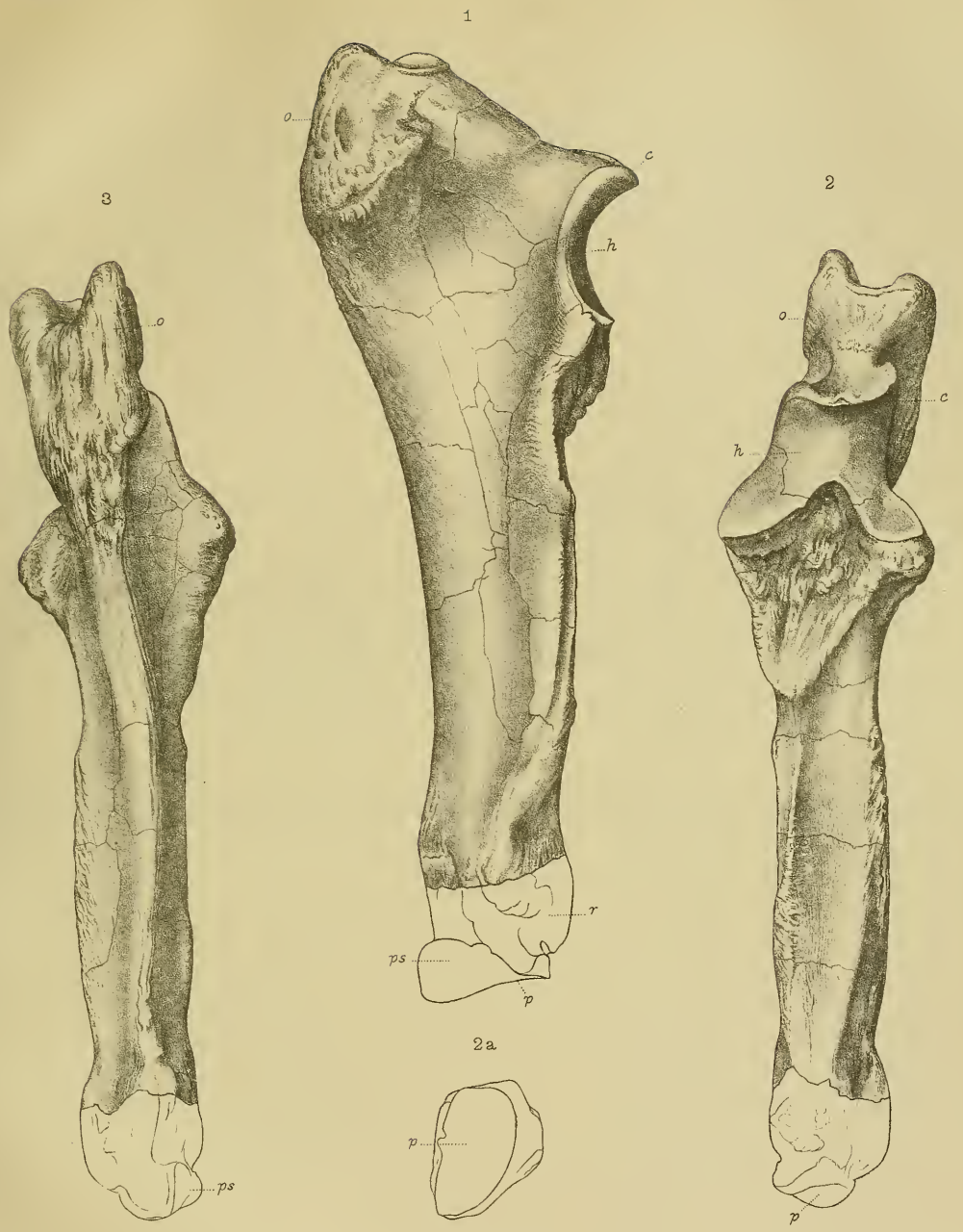
PLATE CCVII

PLATE CCVII

Left Ulna of the Type of Brontops robustus Mersh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 668)

1, Medial or inner view; 2, anterior view; 3, posterior view. *c*, Anconaeal process; *h*, great sigmoid cavity; *o*, olecranon; *p*, facet for cuneiform (pyramidal); *ps*, facet for pisiform. 2a, Distal end. The principal muscle attachments of the ulna are given on page 716.



LEFT ULNA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCVIII

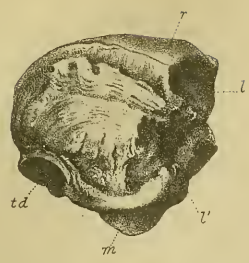
PLATE CCVIII

Left Scaphoid of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Inner or radial view; 2, posterior view; 3, outer or ulnar view; 4, anterior view; 5, proximal surface; 6, distal surface. *l*, *l'*, Facets for articulation with lunar; *m*, facet for articulation with magnum; *r*, facet for articulation with radius; *td*, facet for articulation with trapezoid. The ligamentous attachments of the scaphoid are given on page 716.

4



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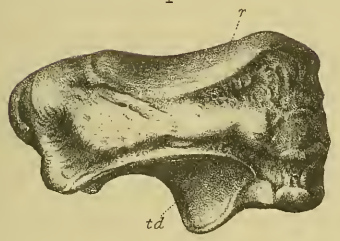

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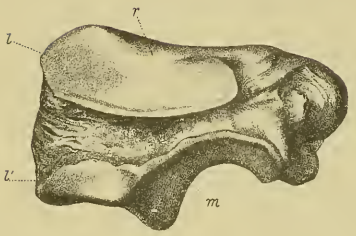

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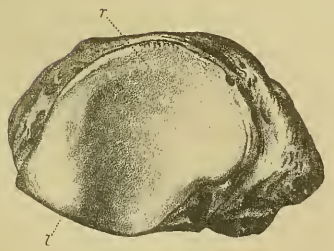

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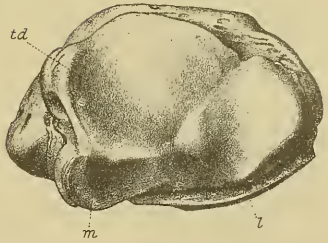

LEFT SCAPHOID OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCIX

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PLATE CCIX

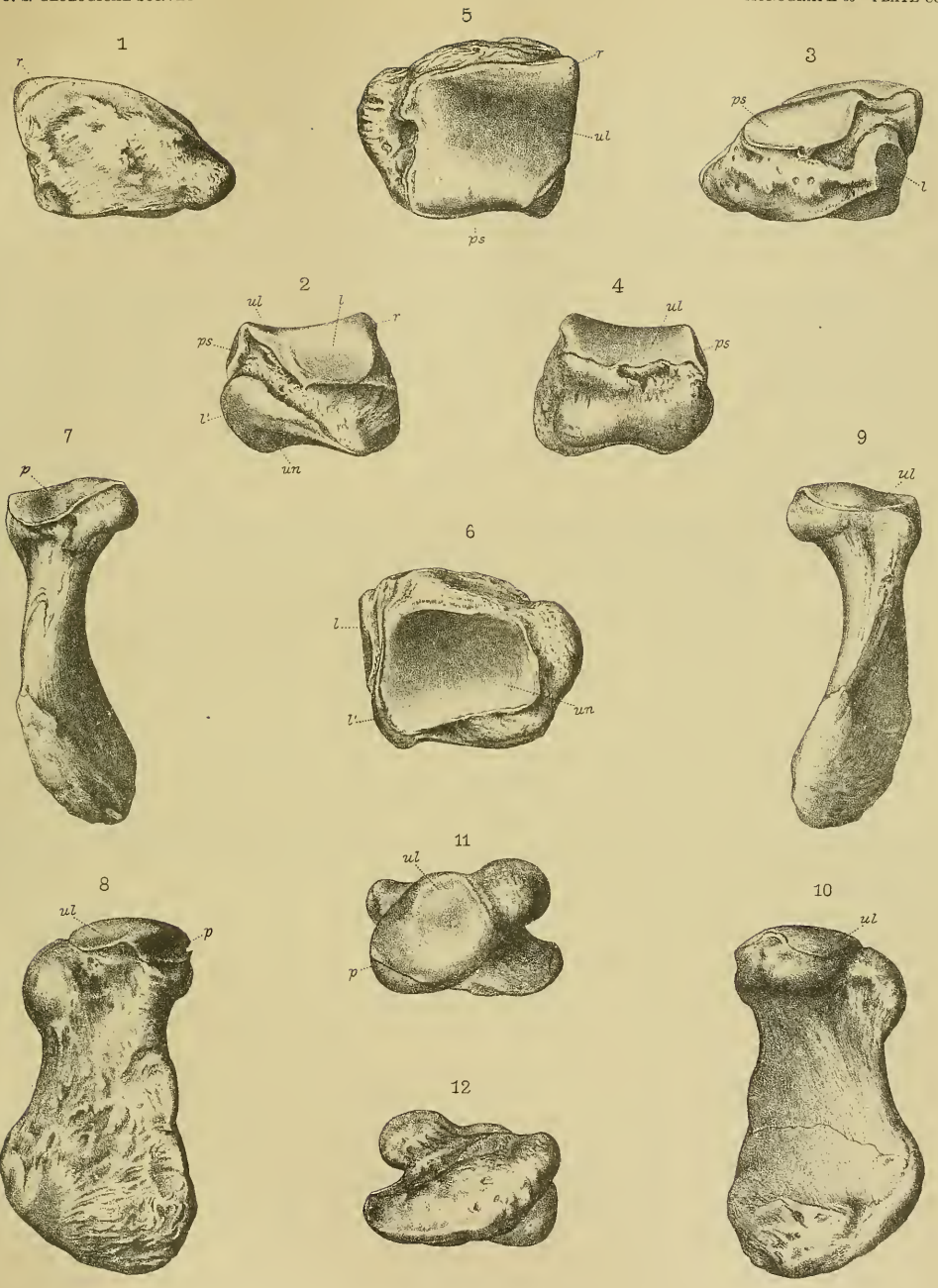
Left Cuneiform Carpi (Pyramidal) and Right Pisiform of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Left pyramidal bone, anterior view; 2, the same, medial or inner view (radial side); 3, the same, posterior view; 4, the same, lateral or outer view (ulnar side); 5, the same, proximal end; 6, the same, distal end. *l–l′*, Facets for articulation with lunar, *r*, facet for articulation with radius; *ps*, facet for articulation with pisiform; *ul*, facet for articulation with ulna; *un*, facet for articulation with unciform.

7, Right pisiform bone, inferior view; 8, the same, lateral or outer view (ulnar side); 9, the same, superior view; 10, the same, medial or inner view (radial side); 11, the same, proximal end; 12, the same, distal end. *p*, Facet for articulation with pyramidal; *ul*, facet for articulation with ulna.

The ligamentous attachments of these elements are given on page 716.



LEFT CUNEIFORM CARPI AND RIGHT PISIFORM OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCX

PLATE CCX

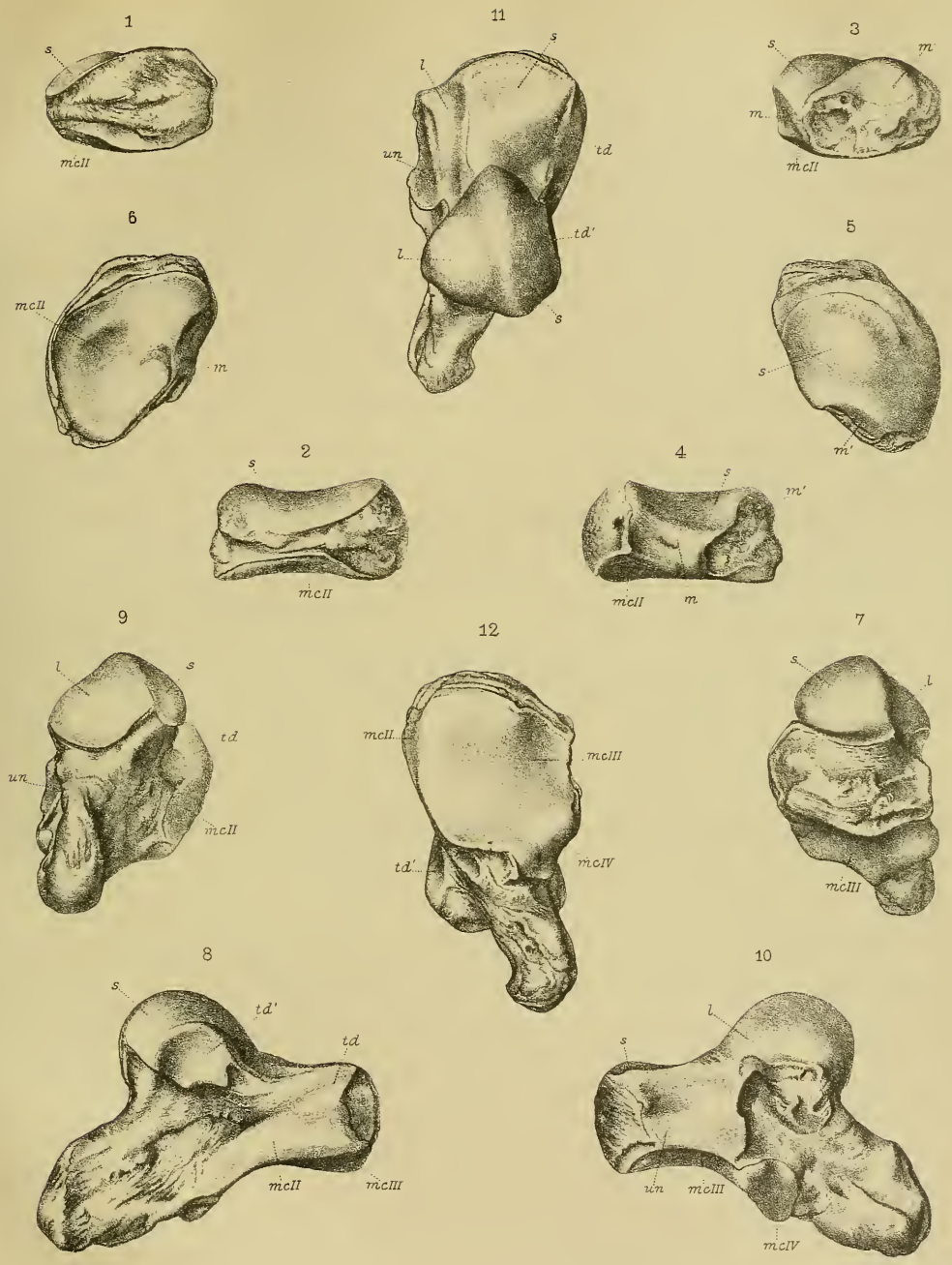
Left Trapezoid and Left Magnum of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Left trapezoid, anterior view; 2, the same, medial or inner view (radial side); 3, the same, posterior view; 4, the same, lateral or outer view (ulnar side); 5, the same, proximal end; 6, the same, distal end. *m*, *m'*, Facets for articulation with magnum; *mcII*, facet for articulation with second metacarpal; *s*, facet for articulation with scaphoid.

7, Left magnum, anterior view; 8, the same, medial or inner view (radial side); 9, the same, posterior view; 10, the same, lateral or outer view (ulnar side); 11, the same, proximal view; 12, the same, distal view. *l*, Facet for articulation with lunar; *mcII*, facet for articulation with second metacarpal; *mcIII*, facet for articulation with third metacarpal; *mcIV*, facet for articulation with fourth metacarpal; *s*, facet for articulation with scaphoid; *td*, *td'*, facets for articulation with trapezoid; *un*, facet for articulation with unciform.

The principal ligamentous and muscular attachments of these elements are given on page 716.



LEFT TRAPEZOID AND LEFT MAGNUM OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXI

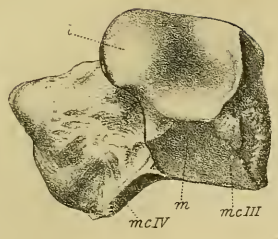
PLATE CCXI

Left Unciform of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Anterior view; 2, medial or inner view (radial side); 3, posterior view; 4, lateral or outer view (ulnar side); 5, proximal view; 6, distal view. *l*, Facet for articulation with lunar; *m*, facet for articulation with magnum; *mcIII*, facet for articulation with third metacarpal; *mcIV*, facet for articulation with fourth metacarpal; *mcV*, facet for articulation with fifth metacarpal; *p*, facet for articulation with cuneiform (pyramidal). The ligamentous and muscular attachments of these elements are given on pages 716, 717.

2



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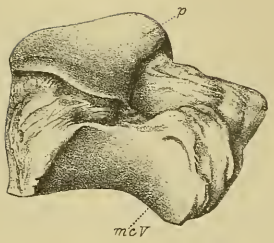

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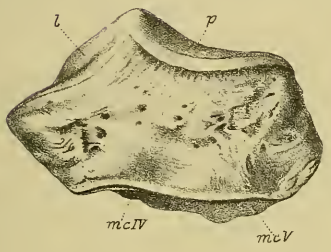

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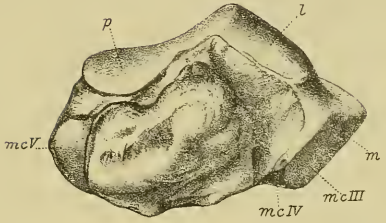

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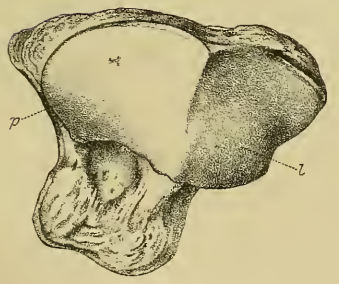

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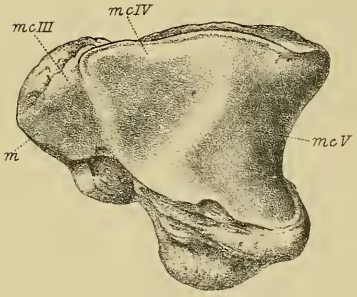


LEFT UNCIFORM OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXII

PLATE CCXII

Second Left Metacarpal of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Anterior view; 1a, section of point indicated by dotted line; 2, medial or inner view (radial side); 3, posterior view; 4, lateral or outer view (ulnar side); 4a, outline of section at point indicated by dotted line; 5, proximal end; 6, distal end. *m*, Facet for articulation with magnum; *mcIII*, facet for articulation with third metacarpal; *ph*, facet for articulation with first phalanx; *s*, facet for articulation with sesamoid; *td*, facet for articulation with trapezoid. The principal ligamentous and muscular attachments of this element are given on pages 716, 717.

SECOND LEFT METACARPAL OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

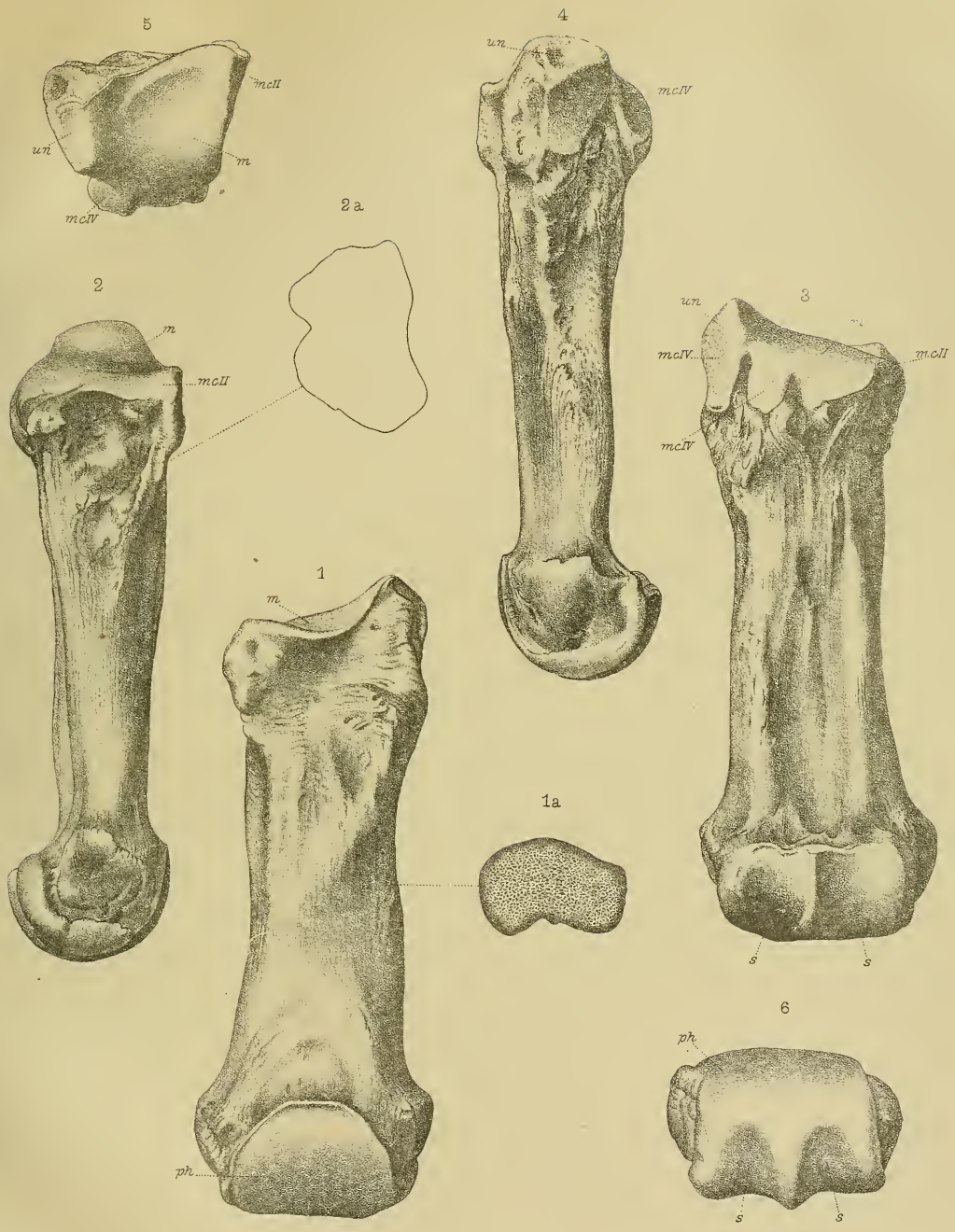
PLATE CCXIII

PLATE CCXIII

Third Left Metacarpal of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Anterior view; 1a, section at point indicated by dotted line; 2, medial or inner view (radial side); 2a, outline of section at point indicated by dotted line; 3, posterior view; 4, lateral or outer view (ulnar side); 5, proximal end; 6, distal end. *m*, Facet for articulation with magnum; *mcII*, facet for articulation with second metacarpal; *mcIV*, facet for articulation with fourth metacarpal; *ph*, facet for articulation with first phalanx; *s*, facet for articulation with sesamoid; *un*, facet for articulation with unciform. The principal ligamentous and muscular attachments of these elements are given on pages 716, 717.



THIRD LEFT METACARPAL OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXIV

PLATE CCXIV

Fourth Left Metacarpal of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Anterior view; 1a, section at point marked by dotted line; 2, medial or inner view (radial side); 2a, outline of section at point indicated by dotted line; 3, posterior view; 4, lateral or outer view (ulnar side); 5, proximal end; 6, distal end. *m*, Facet for articulation with magnum; *mcIII–mcIII'*, facets for articulation with third metacarpal; *mcV*, facet for articulation with fifth metacarpal; *ph*, facet for articulation with first phalanx; *s*, facet for articulation with sesamoid; *un*, facet for articulation with unciform. The principal ligamentous and muscular attachments of this element are given on pages 716, 717.

FOURTH LEFT METACARPAL OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

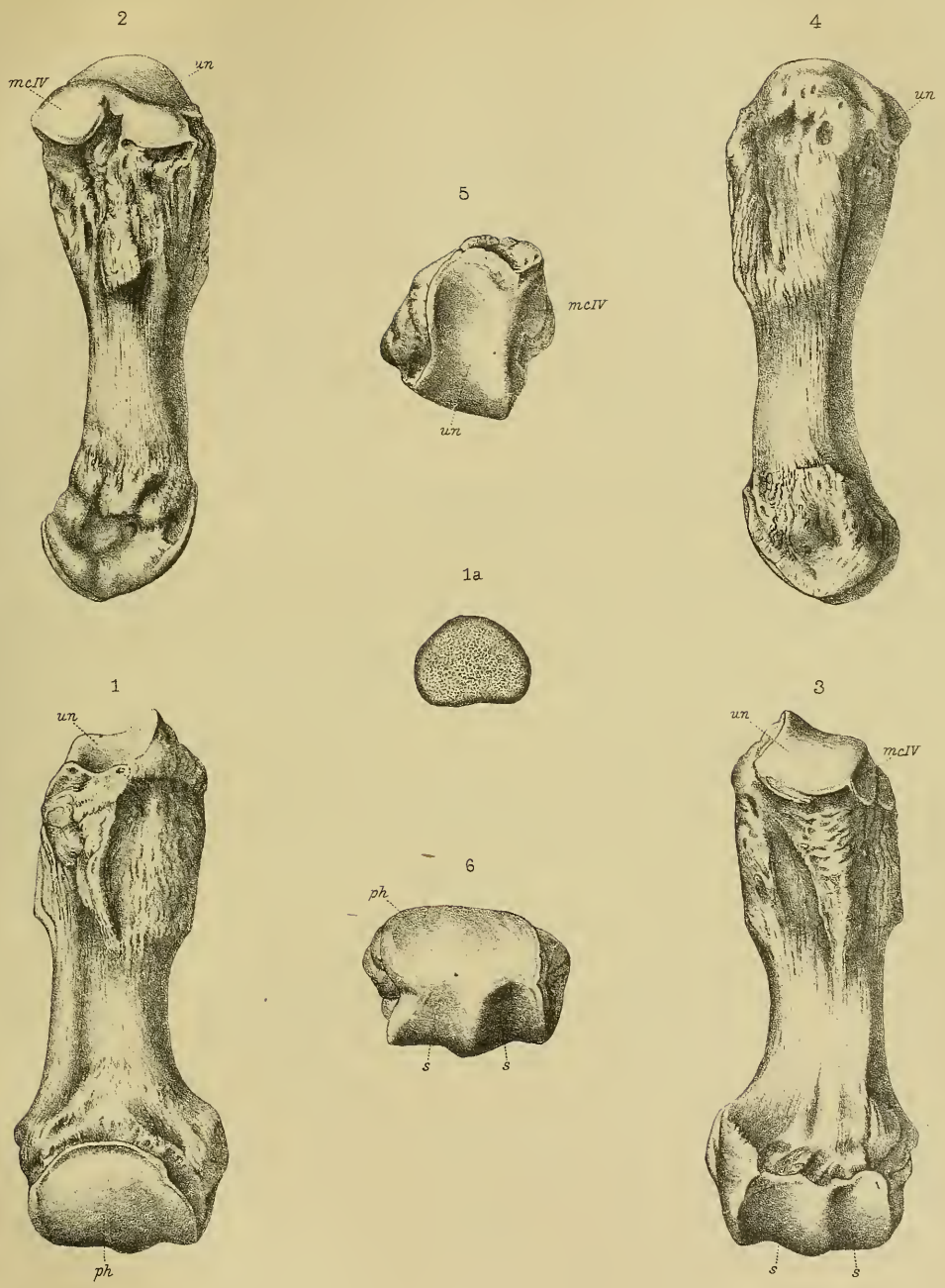
PLATE CCXV

PLATE CCXV

Fifth Left Metacarpal of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Anterior view; 1a, section of shaft; 2, medial or inner view (radial side); 3, posterior view; 4, lateral or outer view (ulnar side); 5, proximal end; 6, distal end. *mcIV*, Facet for articulation with fourth metacarpal; *ph*, facet for articulation with first phalanx; *s*, facet for articulation with sesamoid; *un*, facet for articulation with unciform. The principal ligamentous and muscular attachments of this element are given on pages 716, 717.



FIFTH LEFT METACARPAL OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

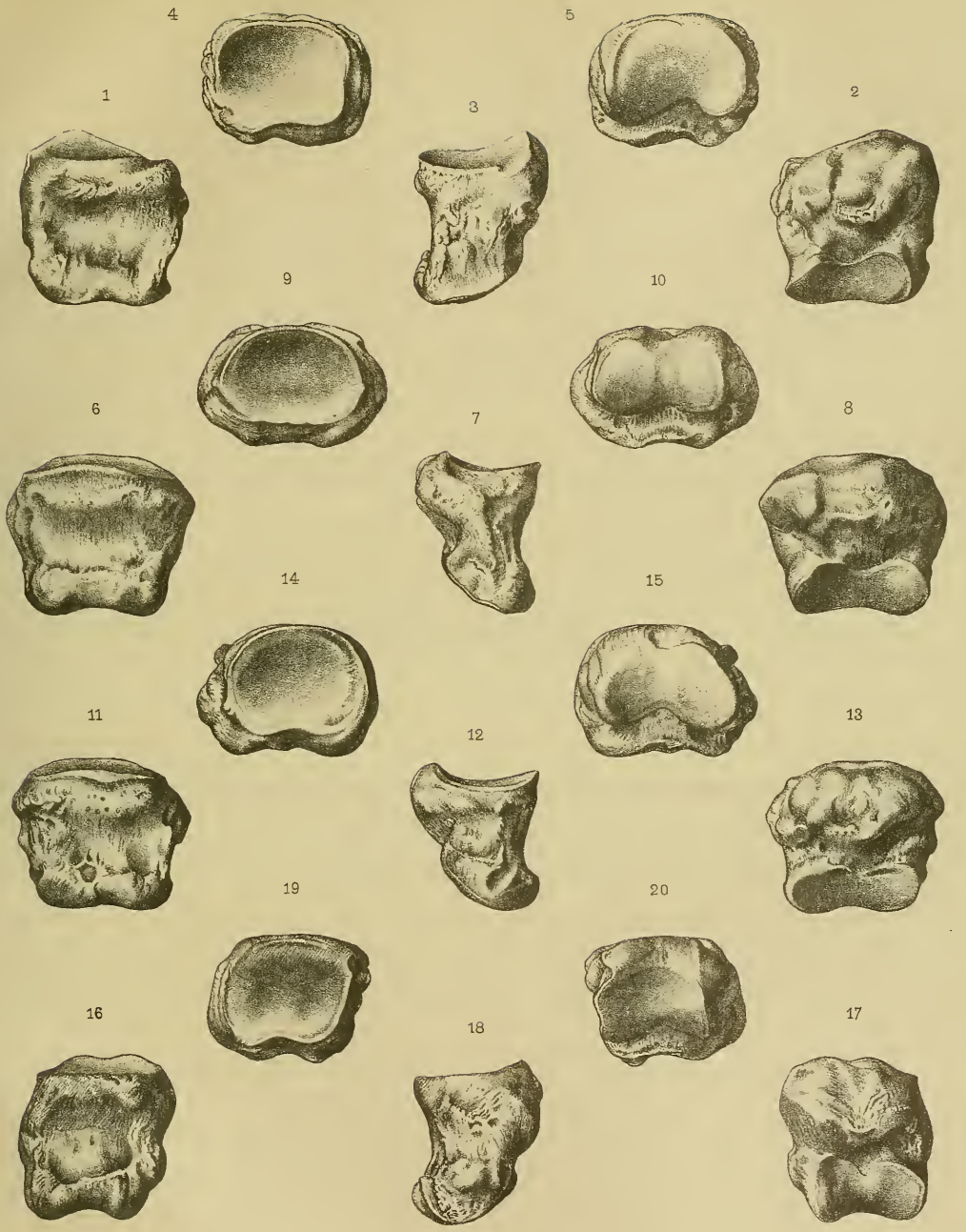
PLATE CCXVI

PLATE CCXVI

Proximal Phalanges of Left Manus of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Proximal phalanx of inner or second digit, anterior view; 2, the same, posterior view; 3, the same, lateral or outer view; 4, the same, proximal end; 5, the same, distal end; 6, proximal phalanx of third digit, anterior view; 7, the same, medial or inner view; 8, the same, posterior view; 9, the same, proximal end; 10, the same, distal end; 11, proximal phalanx of fourth digit, anterior view; 12, the same, medial or inner view; 13, the same, posterior view; 14, the same, proximal end; 15, the same. distal end; 16, proximal phalanx of outer or fifth digit, anterior view; 17, the same, posterior view; 18, the same, lateral or outer view; 19, the same, proximal end; 20, the same, distal end. The principal ligamentous and muscular attachments of this element are given on page 717.



PROXIMAL PHALANGES OF LEFT MANUS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXVII

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PLATE CCXVII

Phalanges and Sesamoids of Manus of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 668)

1, Second phalanx of second(?) digit, lateral or outer view; 2, the same, anterior view; 3, the same, medial or inner view; 4, the same, posterior view; 5, the same, proximal view; 6, the same, distal view; 7, distal phalanx of second(?) digit, lateral or outer view; 8, the same, anterior view; 9, the same, medial or inner view; 10, the same, posterior view; 11, the same, proximal or superior view; 12, the same, distal or inferior view; 13, metacarpal sesamoid of second(?) digit, lateral or outer view; 14, the same, anterior view; 15, the same, medial or inner view; 16, the same, posterior view; 17, the same, end view; 18, phalangeal sesamoid of second(?) digit, medial or inner view; 19, the same, posterior view; 20, the same, anterior view; 21, the same, proximal view; 22, the same, distal view. The principal ligamentous and muscular attachments of these elements are given on page 717.

PHALANGES AND SESAMOIDS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXVIII

PLATE CCXVIII

Pelvis and Sacrum of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. Front view. One-fourth natural size. (See pp. 668, 694)

a, Acetabulum; *c*, crest of ilium; *f*, *f*, obturator fenestra; *il*, ilium; *is*, ischium; *p*, pubis; *s*, sacrum; *z*, prezygapophysis of first sacral vertebra.

PELVIS AND SACRUM OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

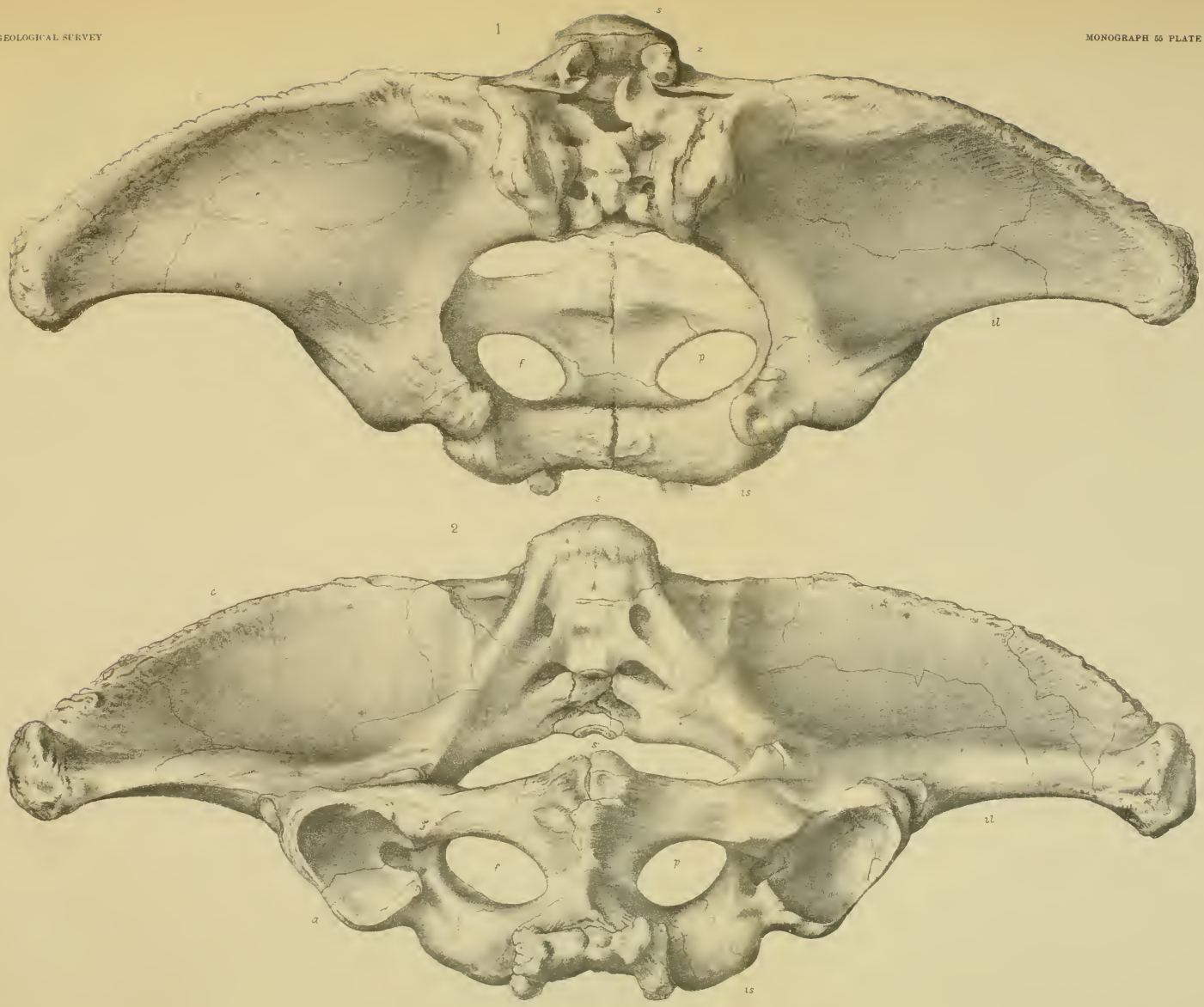
PLATE CCXIX

PLATE CCXIX

Pelvis and Sacrum of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See pp. 668, 694)

1, Superior view; 2, inferior view. *a*, Acetabulum; *c*, crest of ilium; *f*, *f*, obturator fenestra; *is*, ischium; *p*, pubis; *s*, sacrum; *s'*, caudo-sacral vertebra; *z*, prezygapophysis of first sacral vertebra.



PELVIS AND SACRUM OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

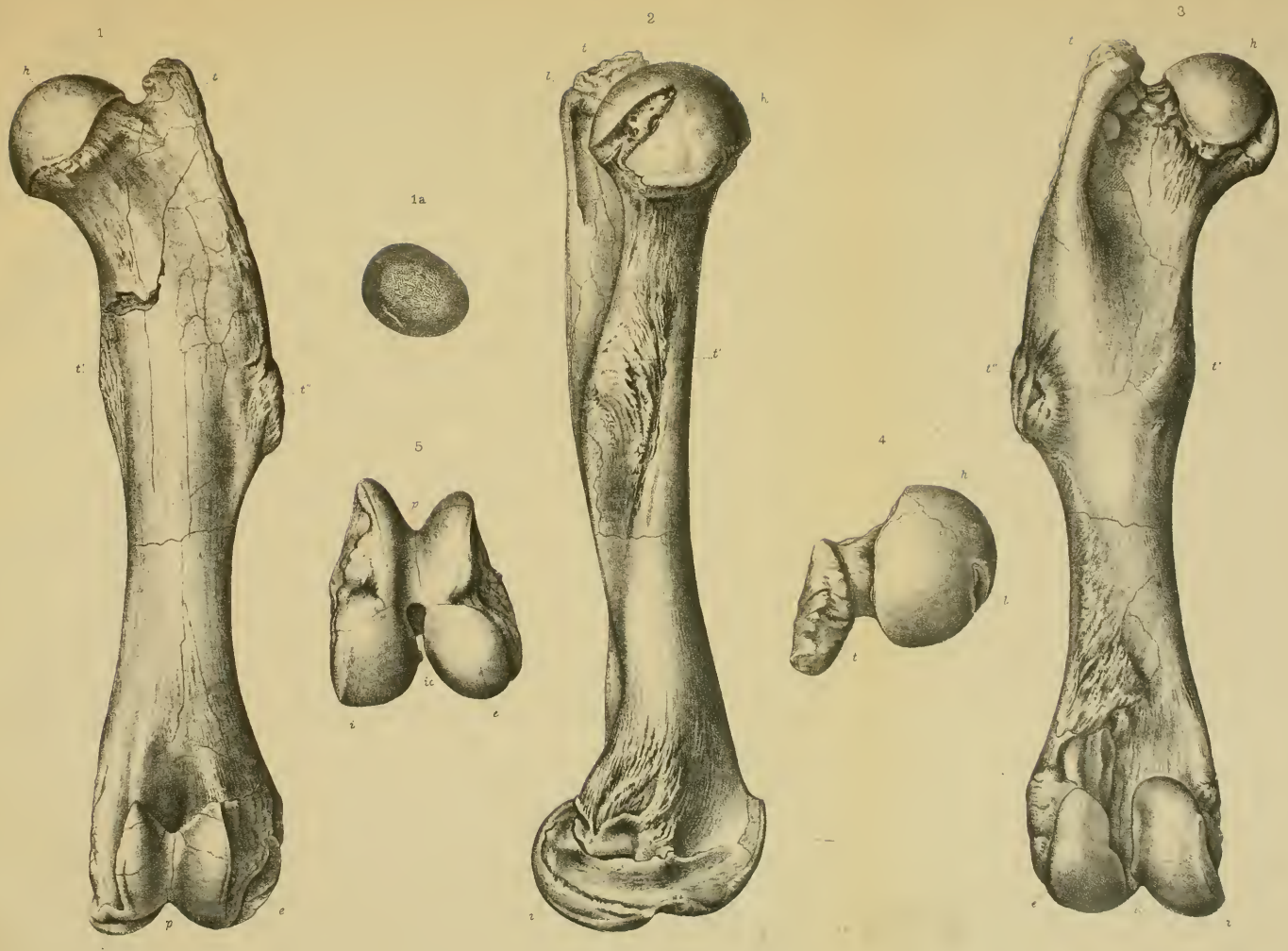
PLATE CCXX

PLATE CCXX

Left Femur of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 668)

1, Anterior view; 1a, section of shaft at break near middle; 2, medial or inner view; 3, posterior view; 4, proximal end; 5, distal end. *e*, Outer condyle; *h*, head of femur; *i*, inner condyle; *ic*, intercondylar notch; *l*, pit for ligamentum teres; *p*, facet for articulation with patella; *t*, great trochanter; *t'*, lesser trochanter; *t''*, third trochanter. The principal ligamentous and muscular attachments of the femur are given on page 719.



LEFT FEMUR OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXXI

PLATE CCXXI

Left Tibia of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 669)

1, Anterior view; 1a, section of shaft at break near middle; 2, medial or inner view; 3, posterior view; 4, lateral or outer view, showing fibular side; 5, proximal end; 6, distal end. *a*, Facet for articulation with astragalus; *e*, facet for articulation with outer condyle of femur; *f*, *f'*, facets for articulation with fibula; *i*, facet for articulation with inner condyle; *p*, procnemial ridge; *s*, spine of tibia. The principal ligamentous and muscular attachments of the tibia are given on page 720.

LEFT TIBIA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXXII

PLATE CCXXII

Left Patella and Left Fibula of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 669)

1, Left patella, anterior view; 2, the same, medial or inner view; 3, the same, posterior view; 4, the same, lateral or outer view. *f*, Facet for articulation with femur.

5, Left fibula, lateral or outer view; 5a, the same, section of shaft at break near middle; 6, the same, anterior view; 7, the same, medial or inner view; 8, the same, posterior view. *a*, Facet for articulation with astragalus; *c*, facet for articulation with calcaneum; *t*, *t'*, facets for articulation with tibia. The principal ligamentous and muscular attachments of the fibula are given on page 720.

LEFT PATELLA AND LEFT FIBULA OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

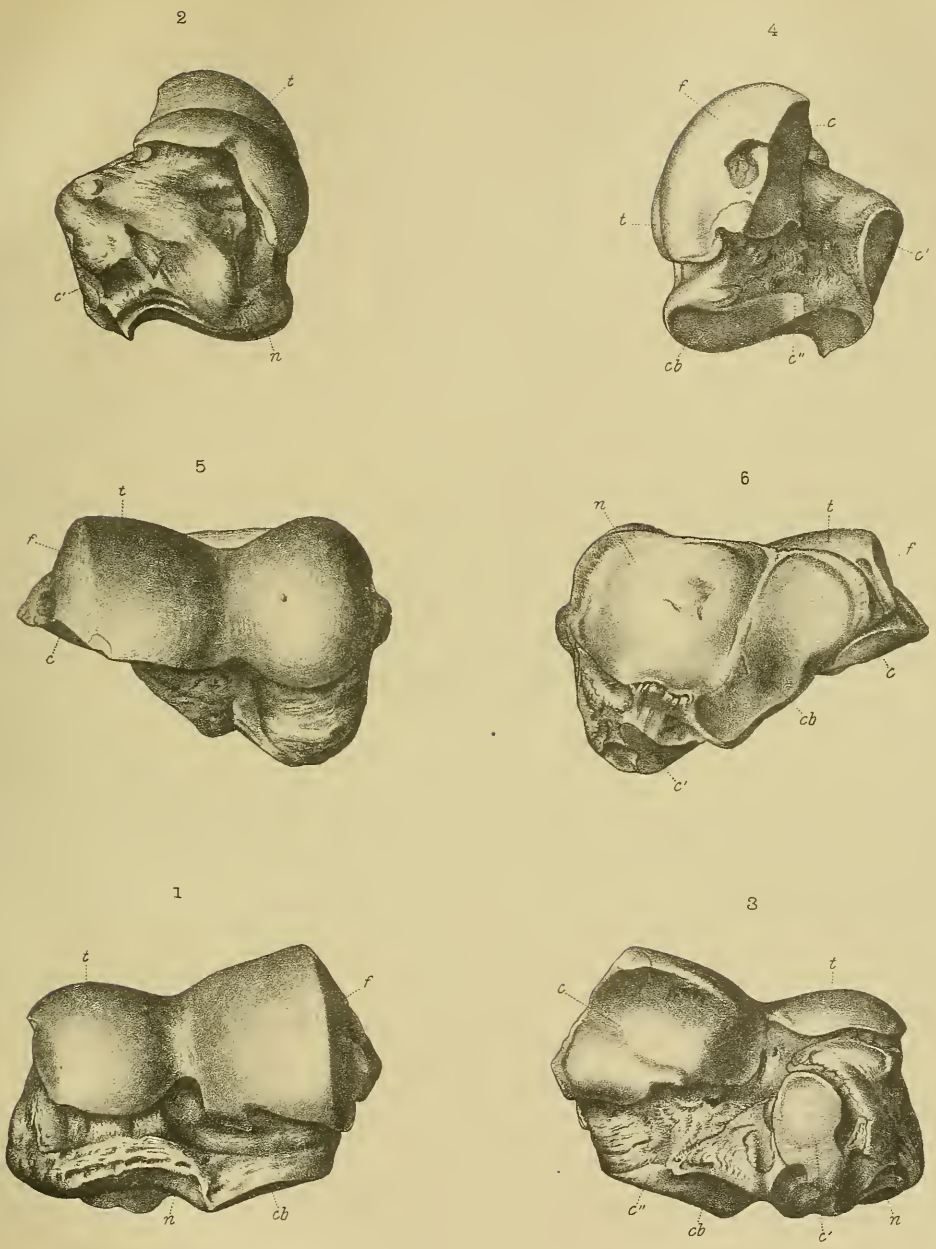
PLATE CCXXIII

PLATE CCXXIII

Left Astragalus of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 669)

1, Anterior view; 2, medial or inner view (tibial side); 3, posterior view; 4, lateral or outer view (fibular side); 5, proximal view; 6, distal view. *c*, Ectal; *c'*, sustentacular; *c''*, distal facets for calcaneum; *cb*, cuboid facet; *f*, fibular facet; *n*, navicular facet; *t*, tibial facet. The ligamentous attachments of the astragalus are given on page 724.



LEFT ASTRAGALUS OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

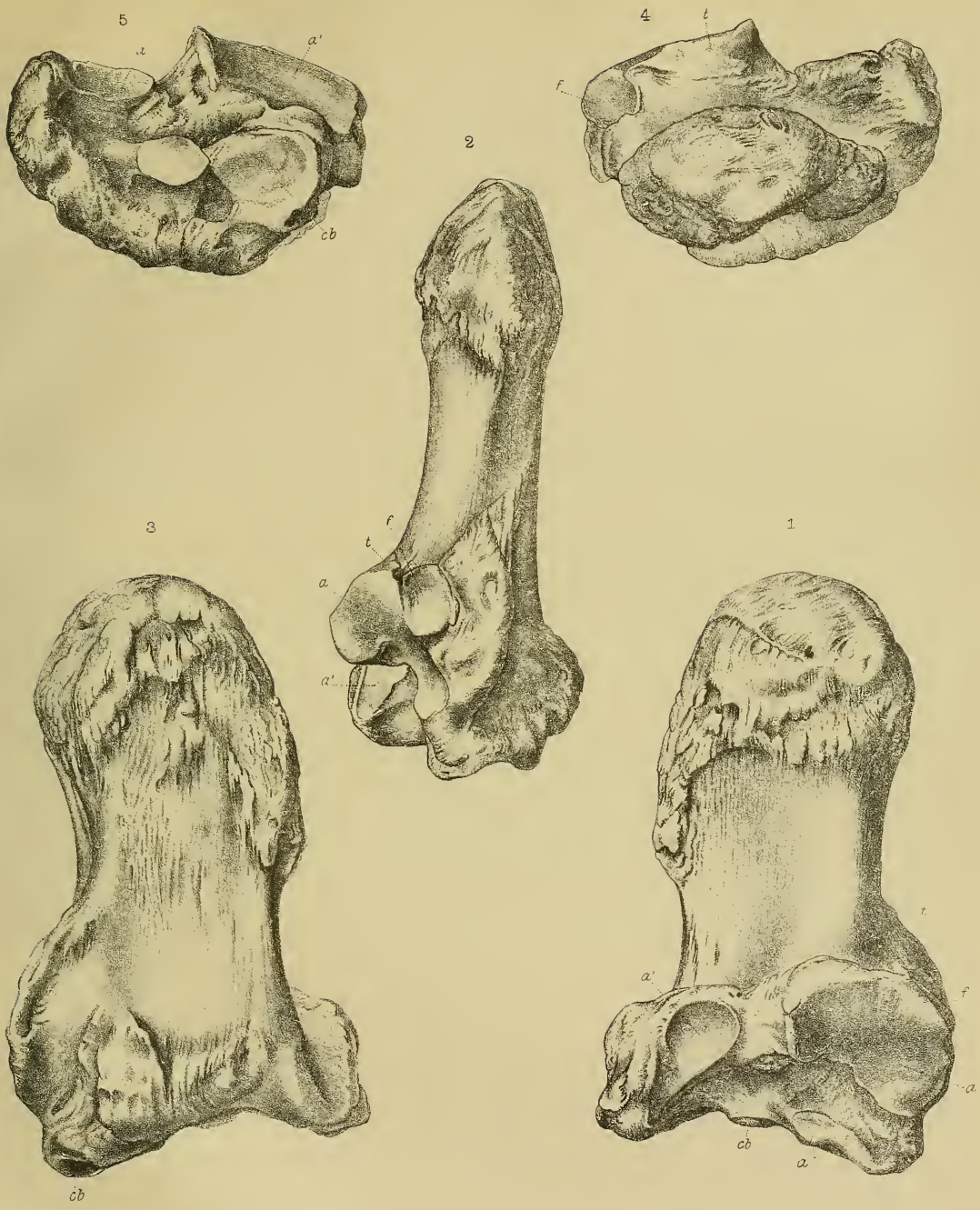
PLATE CCXXIV

PLATE CCXXIV

Left Calcaneum of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 669)

1, Anterosuperior view; 2, external view; 3, postero-inferior view; 4, proximal view; 5, distal view. *a*, Astragalar facet; *a'*, sustentacular facet; *a''*, distal astragalar facet; *cb*, cuboid facet; *f*, fibular facet; *t*, tibial facet. The principal ligamentous and muscular attachments of the calcaneum are given on pages 721, 722.



LEFT CALCANEUM OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXXV

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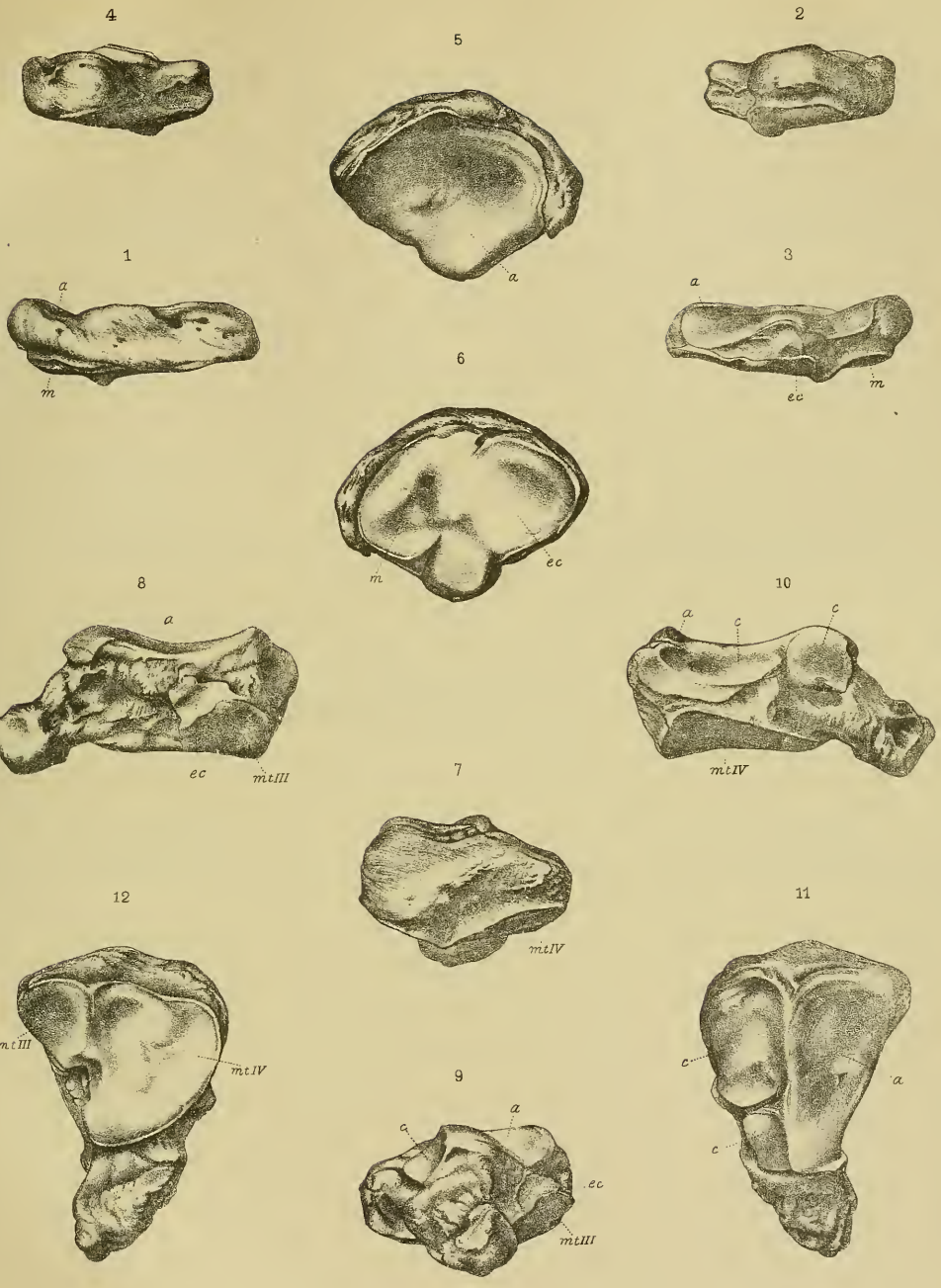
PLATE CCXXV

Left Navicular and Left Cuboid of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 669)

1, Left navicular, external view; 2, the same, internal view; 3, the same, posterior view; 4, the same, external view; 5, the same, superior view; 6, the same, inferior view; 7, left cuboid, anterior view; 8, the same, internal view; 9, the same, posterior view; 10, the same, external view; 11, the same, superior view; 12, the same, inferior view. *a*, Astragalar facet; *c*, calcanear facet; *ec*, ectocuneiform facet; *m*, mesocuneiform facet; *mtIII*, facet for metacarpal III; *mtIV*, facet for metacarpal IV. The principal ligamentous and muscular attachments of these elements are given on page 724.



LEFT NAVICULAR AND LEFT CUBOID OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

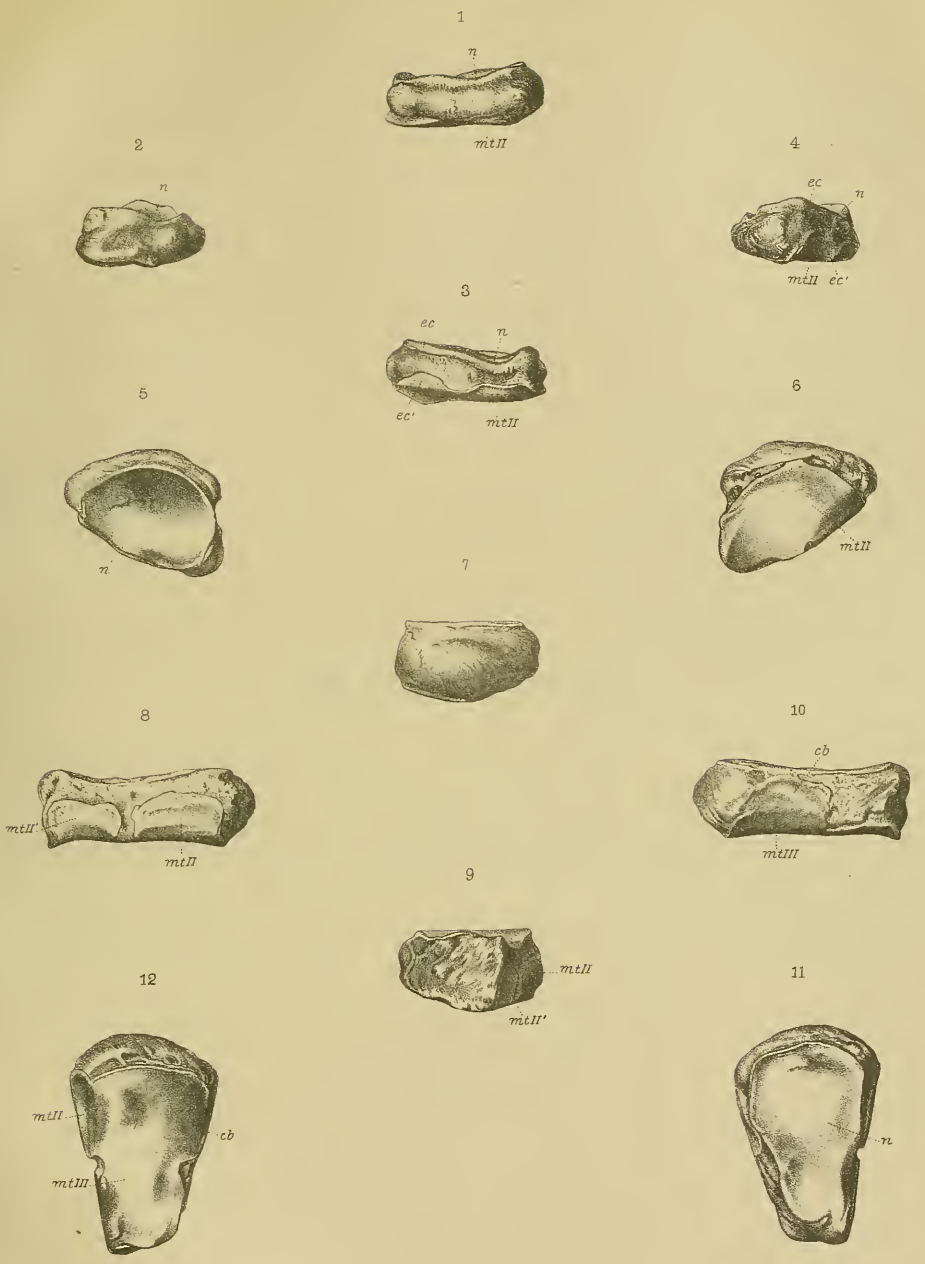
PLATE CCXXVI

PLATE CCXXVI

Left Ectocuneiform and Left Mesocuneiform of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 669)

1, Left mesocuneiform, anterior view; 2, the same, internal view; 3, the same, posterior view; 4, the same, external view; 5, the same, superior view; 6, the same, inferior view; 7, left ectocuneiform, anterior view; 8, the same, internal view; 9, the same, posterior view; 10, the same, external view; 11, the same, superior view; 12, the same, inferior view. *cb*, Cuboid facet; *ec*, *ec'*, facets for ectocuneiform; *mtII*, *mtII'*, facets for metatarsal II; *mtIII*, facet for metatarsal III; *n*, navicular facet. The principal ligamentous and muscular attachments of these elements are given on page 724.



LEFT ECTOCUNEIFORM AND LEFT MESOCUNEIFORM
OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

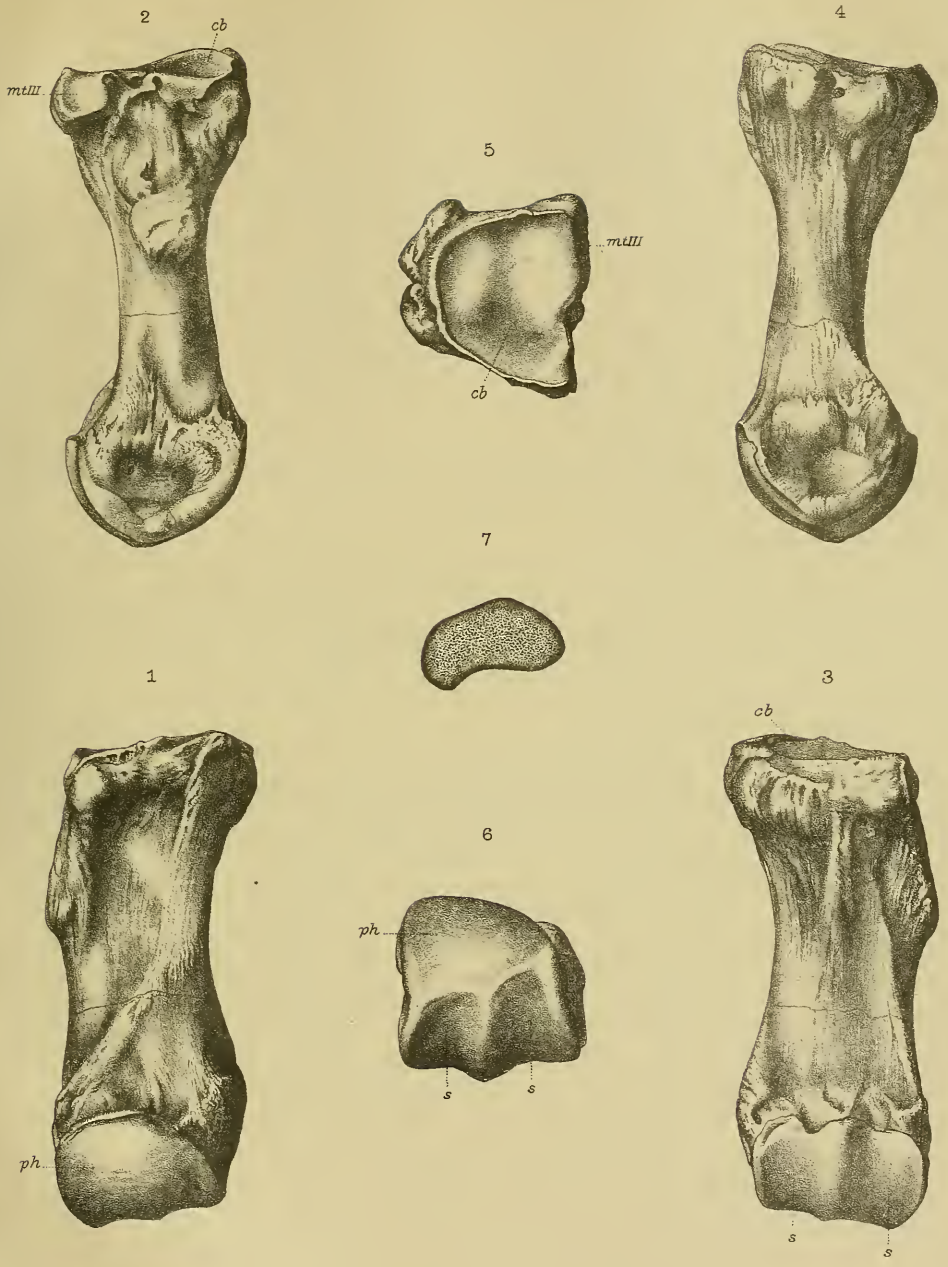
PLATE CCXXVII

PLATE CCXXVII

Left Fourth Metatarsal of the Type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 669)

1, Anterior view; 2, medial or inner view (tibial side); 3, posterior view; 4, lateral or outer view (fibular side); 5, proximal view; 6, distal view; 7, cross section of shaft. *cb*, Facet for cuboid; *mtIII*, facet for third metatarsal; *ph*, facet for proximal phalanx; *s*, *s*, facets for sesamoids. The principal ligamentous and muscular attachments of this element are given on page 724.



LEFT FOURTH METATARSAL OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXXVIII

PLATE CCXXVIII

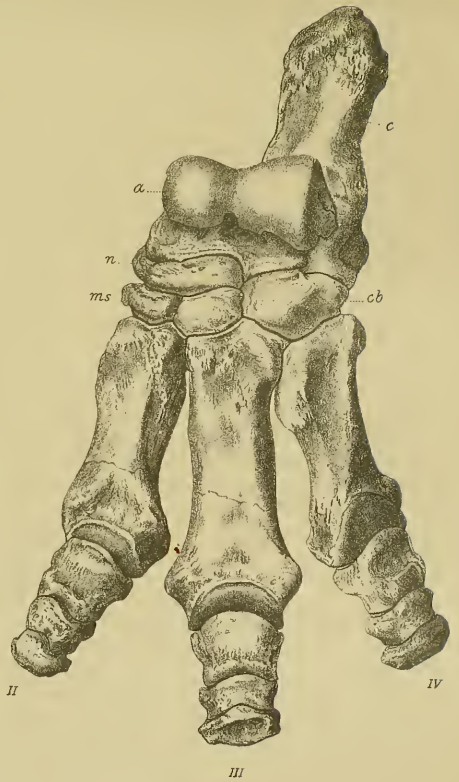
Left Manus and Left Pes of the type of Brontops robustus Marsh

Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See pp. 668, 669)

1, Left manus, anterior view; 2, left pes, anterior view. *a*, Astragalus; *c*, calcaneum; *cb*, cuboid; *ms*, mesocuneiform; *n*, navicular; *p*, pyramidal (cuneiform); *ps*, pisiform; *R*, radius; *s*, scaphoid; *tr*, trapezium; *U*, ulna; *unc*, unciform; *II*, *III*, *IV*, *V*, digits. The principal ligamentous and muscular attachments of these elements are given on pages 717, 724.

1

2



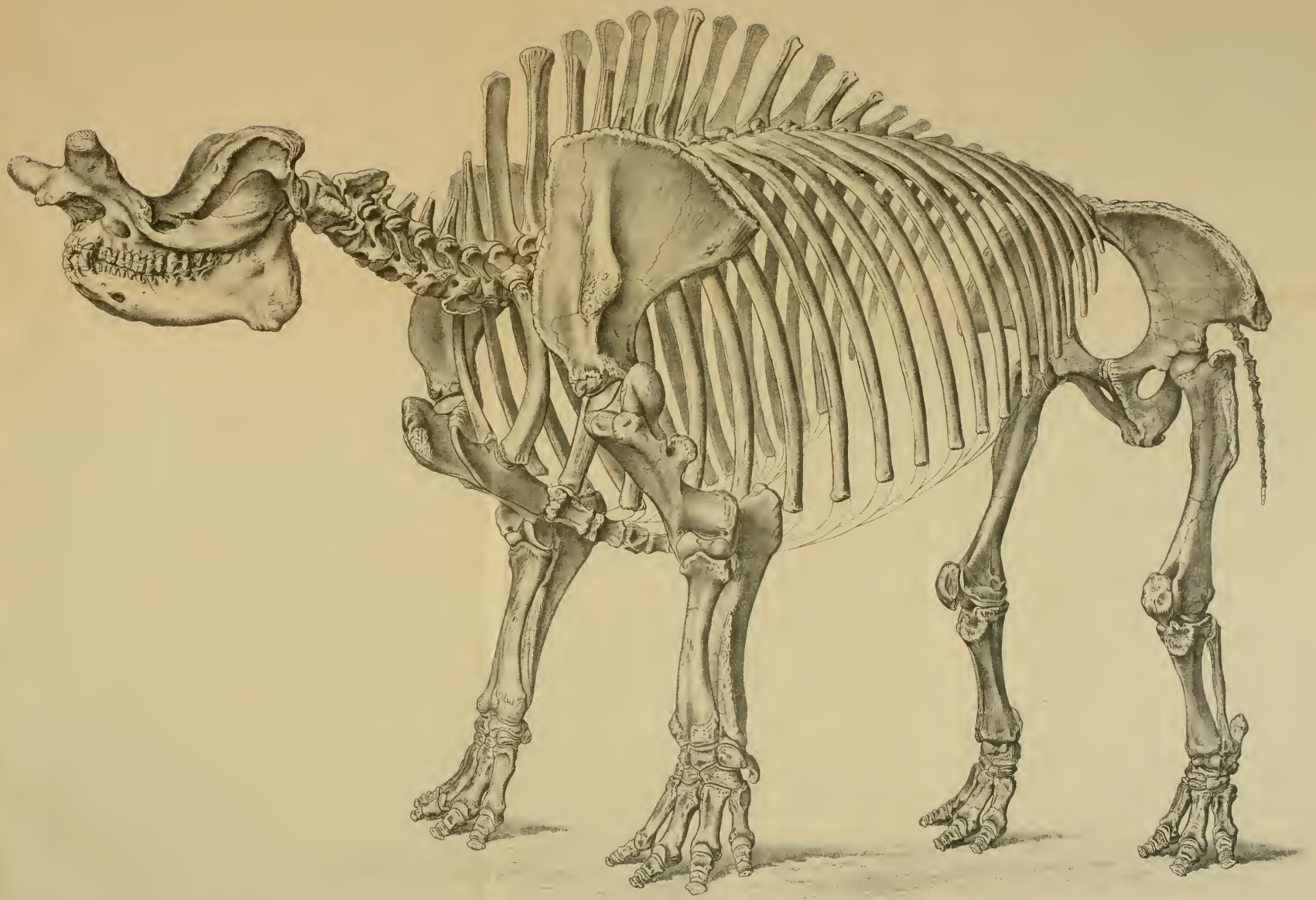
LEFT MANUS AND LEFT PES OF THE TYPE OF BRONTOPS ROBUSTUS MARSH

PLATE CCXXIX

PLATE CCXXIX

RESTORATION OF THE SKELETON OF BRONTOPS ROBUSTUS MARSH

Plate prepared under the direction of Professor Marsh. One-seventh natural size. (See p. 666)



RESTORATION OF THE SKELETON OF BRONTOPS ROBUSTUS MARSH

PLATE CCXXX

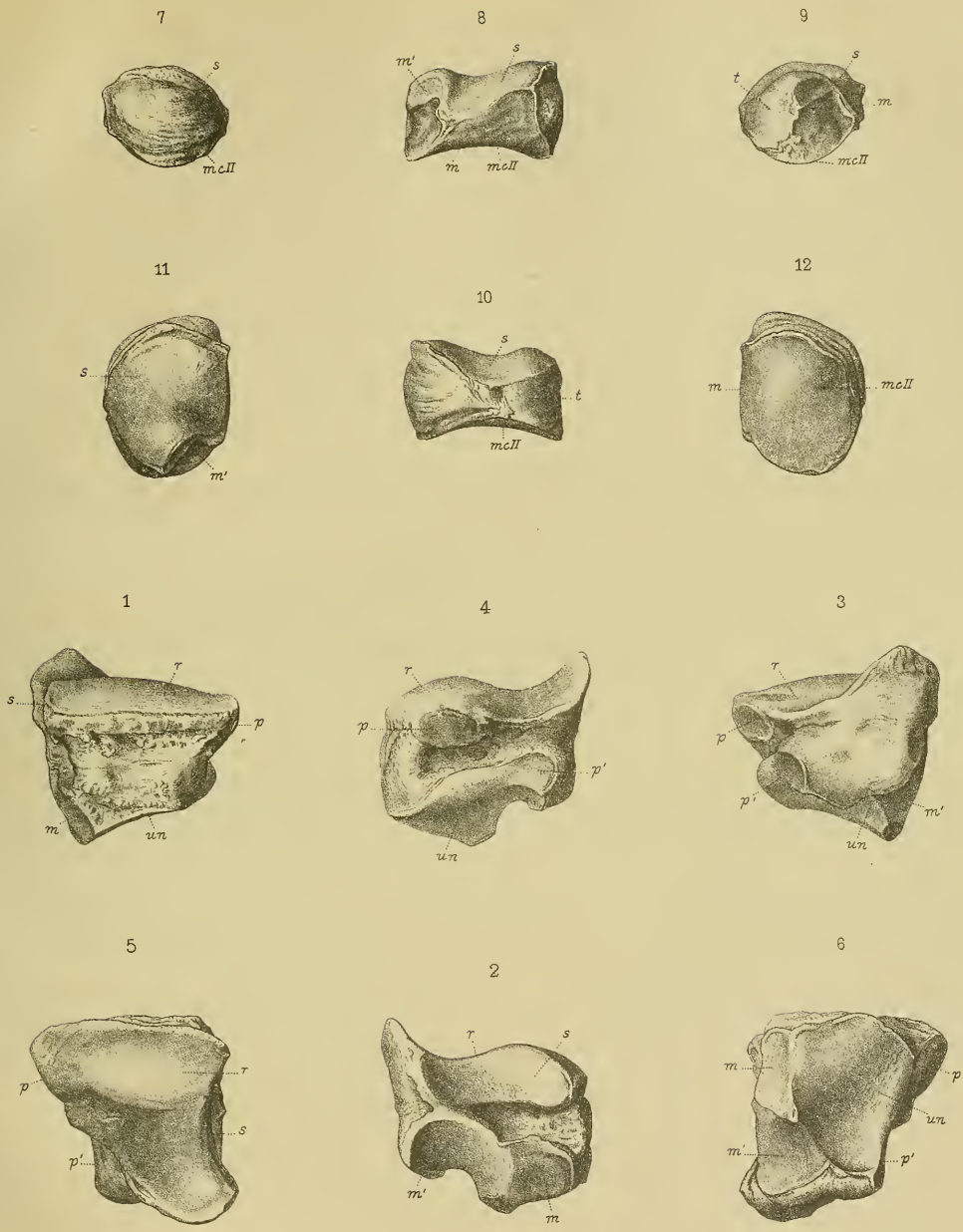
PLATE CCXXX

Left Lunar and Right Trapezoid Referred by Marsh to Brontotherium gigas

May be associated with type. Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 692)

1, Left lunar, anterior view; 2, the same, medial or inner view (radial side); 3, the same, posterior view; 4, the same, lateral or outer view (ulnar side); 5, the same, superior or proximal view; 6, the same, inferior or distal view. *m*, *m'*, Facets for magnum; *p*, *p'*, facets for pryamidal (cuneiform); *r*, facet for radius; *s*, facet for scaphoid; *un*, facet for unciform.

7, Right trapezoid, anterior view; 8, the same, lateral or outer view (ulnar side); 9, the same, posterior view; 10, the same, medial or inner view (radial side); 11, the same, superior or proximal view; 12, the same, inferior or distal view. *m*, *m'*, Facets for magnum; *mcII*, facet for second metacarpal; *p*, *p'*, facets for cuneiform; *r*, facet for radius; *s*, facet for scaphoid; *t*, facet for trapezium; *un*, facet for unciform.



LEFT LUNAR AND RIGHT TRAPEZOID REFERRED BY MARSH TO BRONTOTHERIUM GIGAS

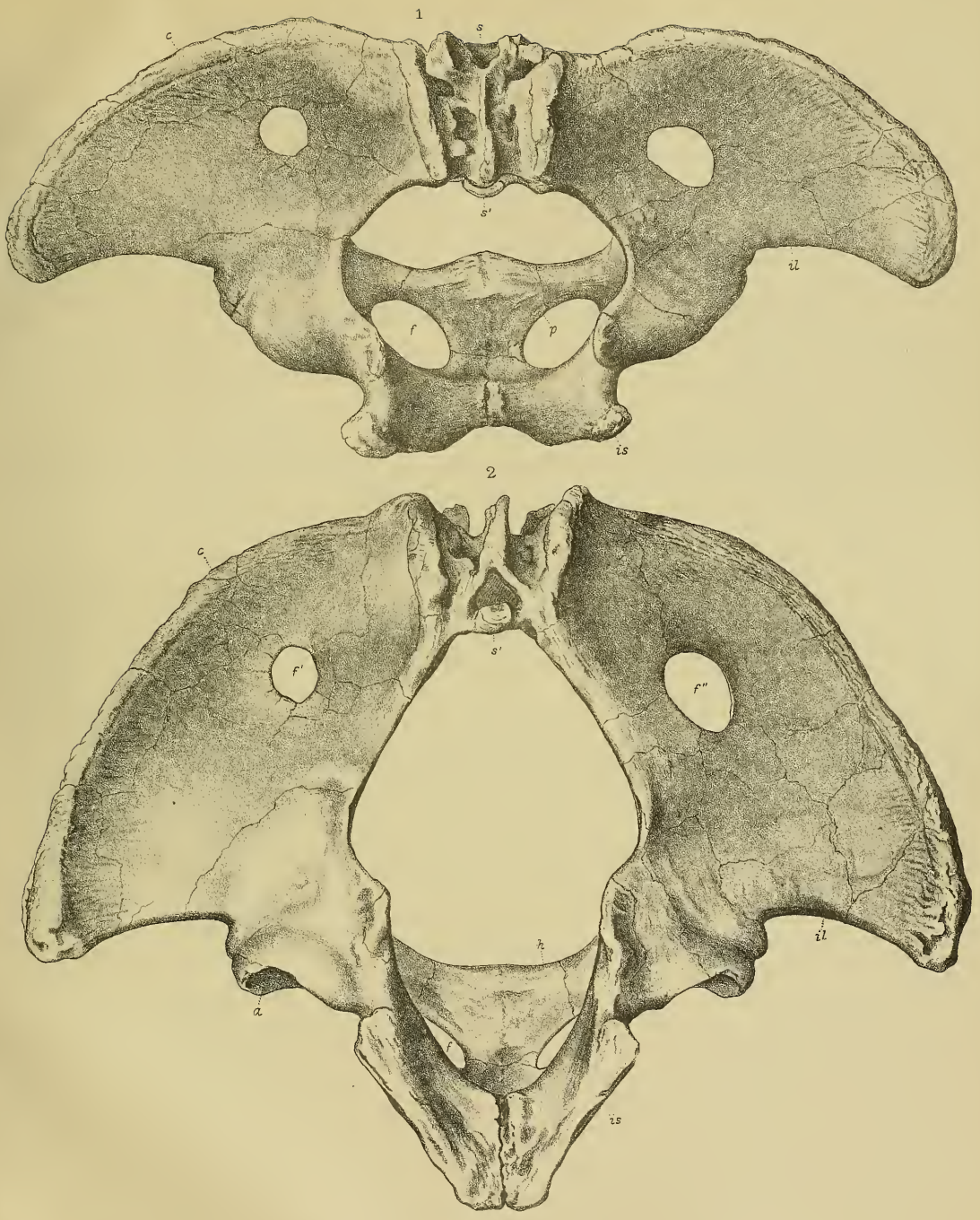
PLATE CCXXXI

PLATE CCXXXI

Pelvis and Sacrum Referred by Marsh to Brontotherium gigas

U. S. National Museum. Plate prepared under the direction of Professor Marsh. One-fourth natural size. (See p. 694)

1, Dorsal view; 2, posterior view. *a*, Acetabulum; *c*, crest of ilium; *f*, thyroid, or obturator foramen; *f'*, *f''*, vacuities, or unossified regions in gluteal surface of ilium; *p*, pubis; *il*, ilium; *is*, ischium; *p*, pubis; *s'*, caudosacral vertebra.



PELVIS AND SACRUM REFERRED BY MARSH TO BRONTOTHERIUM GIGAS

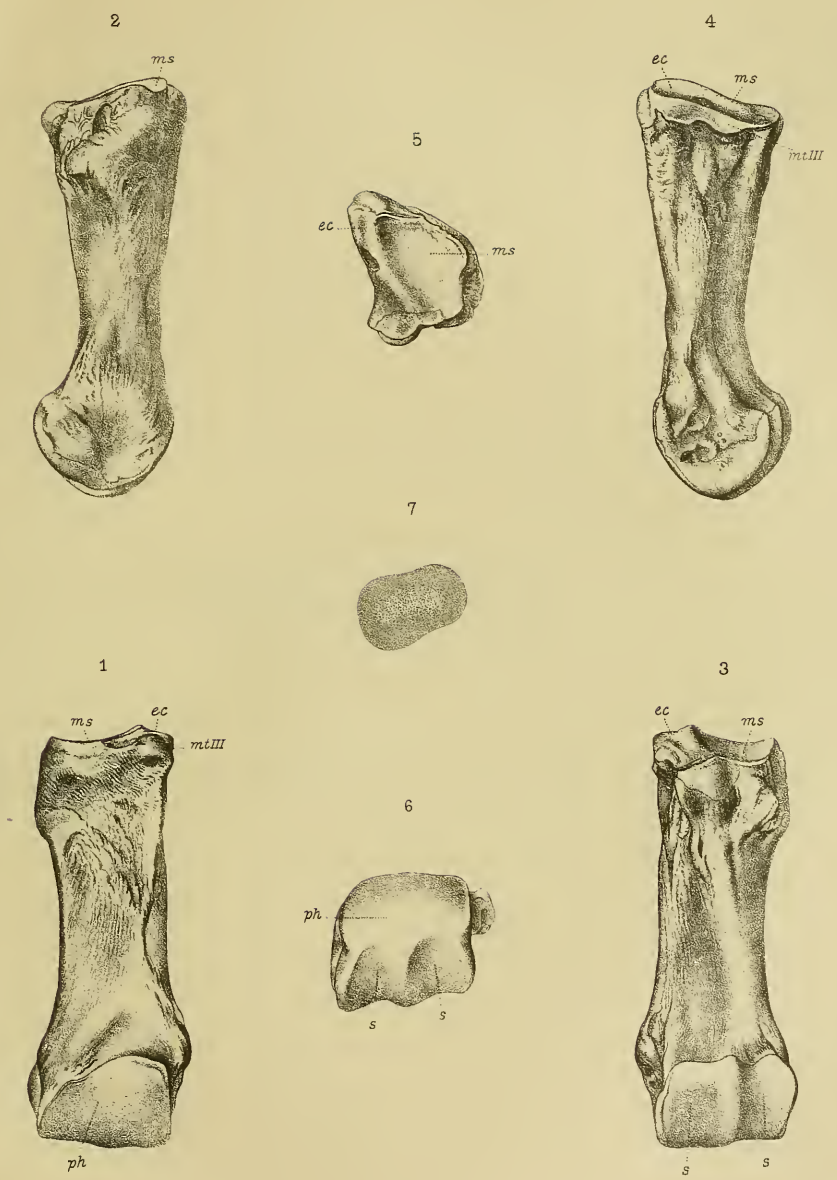
PLATE CCXXXII

PLATE CCXXXII

Left Second Metatarsal Referred by Marsh to Brontotherium gigas

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 694)

1, Anterior view; 2, medial or inner view (tibial side); 3, posterior view; 4, lateral or outer view (fibular side); 5, proximal view; 6, distal view; 7, cross section of shaft. *ec*, Facet for ectocuneiform; *ms*, facet for mesocuneiform; *mtIII*, facet for metatarsal III; *ph*, facet for proximal phalanx; *s*, *s*, facets for sesamoids.



LEFT SECOND METATARSAL REFERRED BY MARSH TO BRONTOTHERIUM GIGAS

PLATE CCXXXIII

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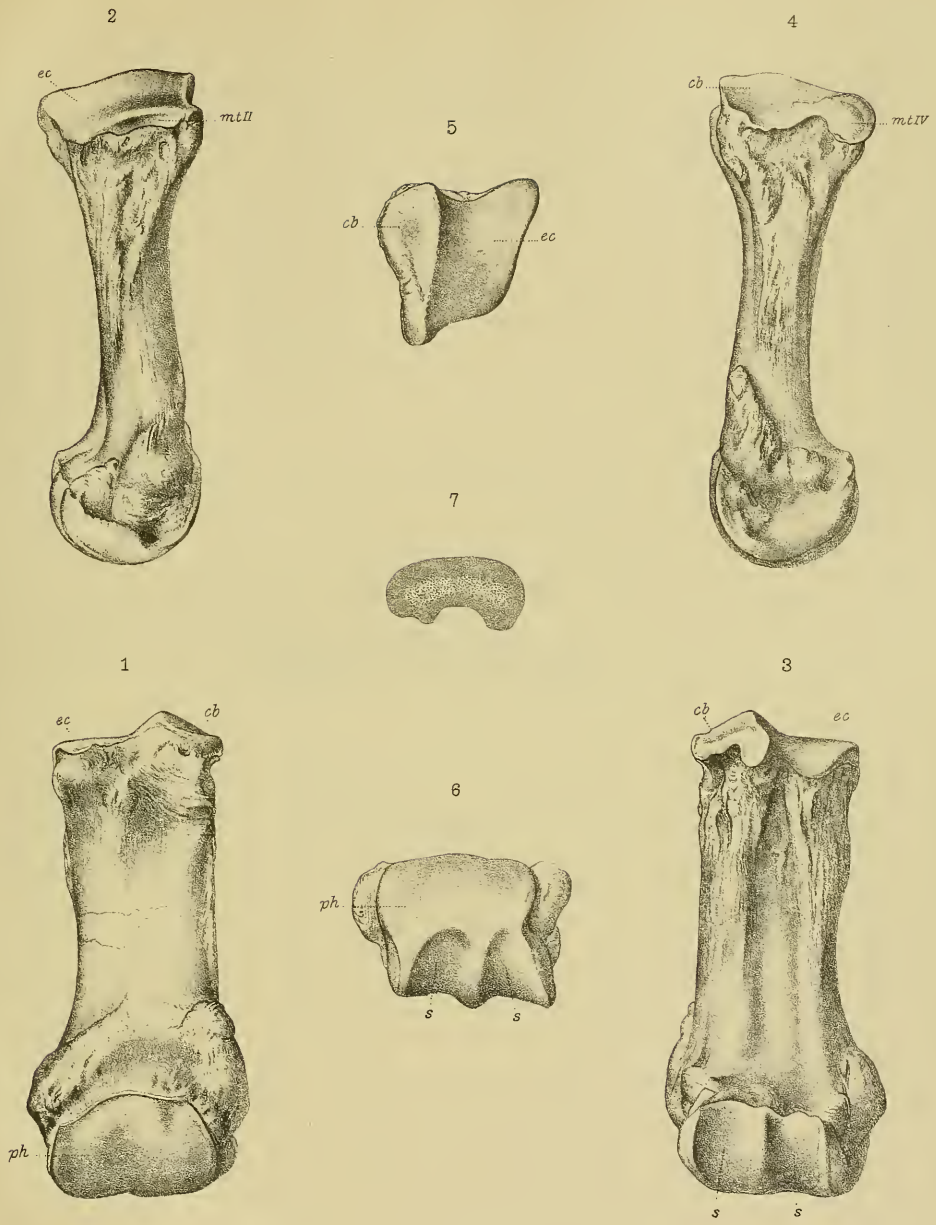
PLATE CCXXXIII

Left Third Metatarsal Referred by Marsh to Brontotherium gigas

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 694)

1, Anterior view; 2, medial or inner view (tibial side); 3, posterior view; 4, lateral or outer view (fibular side); 5, proximal view; 6, distal view; 7, cross section of shaft. *cb*, Facet for cuboid; *ec*, facet for ectocuneiform; *mtIV*, facet for fourth metatarsal *ph*, facet for proximal phalanx; *s*, *s*, facets for sesamoids.



LEFT THIRD METATARSAL REFERRED BY MARSH TO BRONTOTHERIUM GIGAS

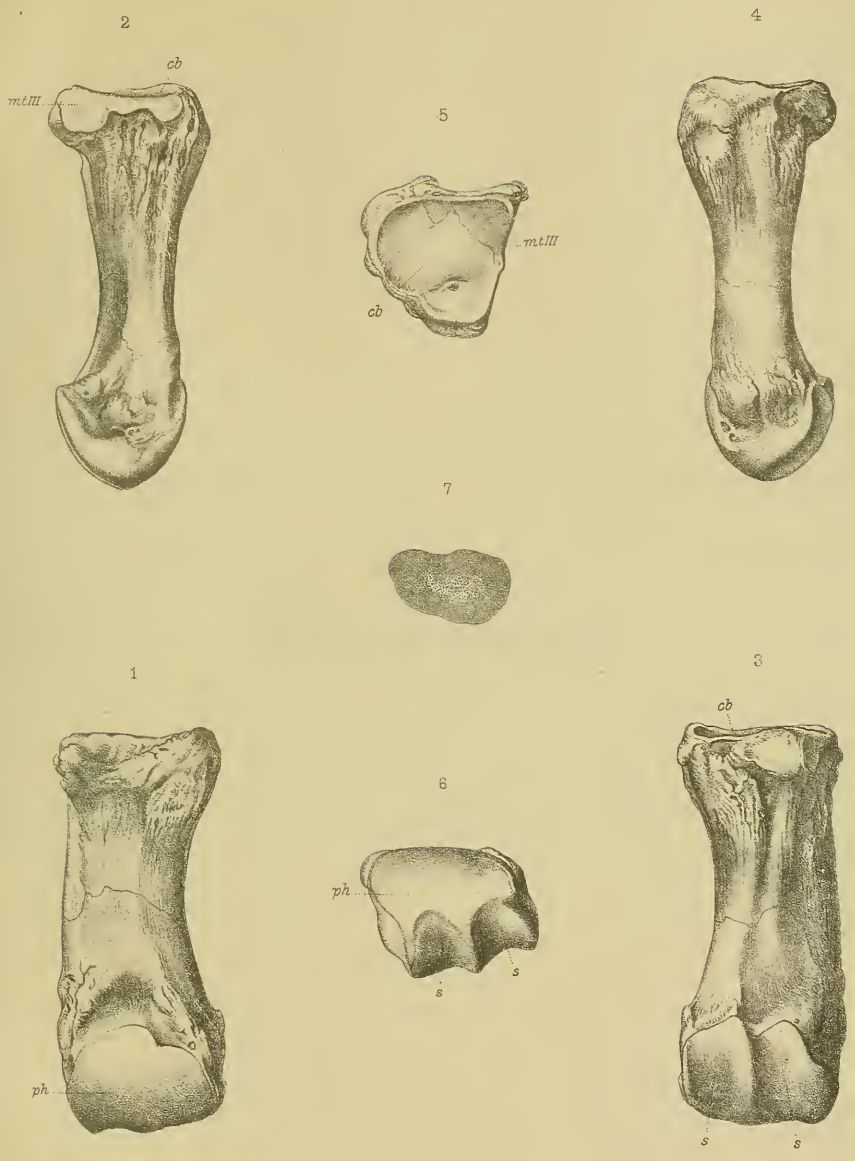
PLATE CCXXXIV

PLATE CCXXXIV

Left Fourth Metatarsal Referred by Marsh to Brontotherium gigas

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 694)

1, Anterior view; 2, medial or inner view (tibial side); 3, posterior view; 4, lateral or outer view (fibular side); 5, proximal view; 6, distal view; 7, cross section of shaft. *cb*, Facet for cuboid; *mtsIII*, facet for median or third metatarsal; *ph*, facet for proximal phalanx; *s*, *s*, facets for sesamoids.



LEFT FOURTH METATARSAL REFERRED BY MARSH TO BRONTOTHERIUM GIGAS

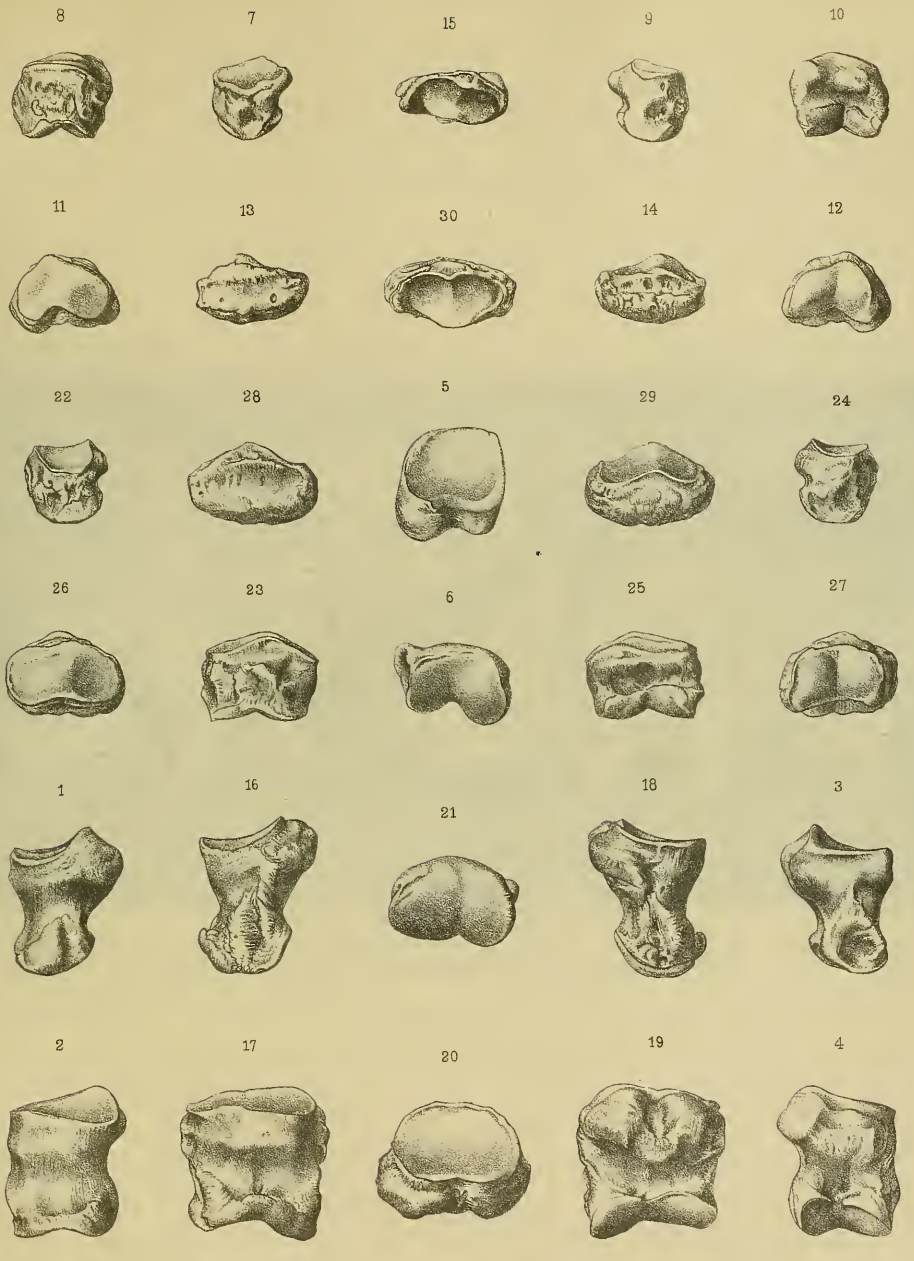
PLATE CCXXXV

PLATE CCXXXV

Phalanges of Left Second, Third, and Fourth Digits Referred by Marsh to Brontotherium gigas

Plate prepared under the direction of Professor Marsh. One-half natural size. (See p. 694)

1, Proximal phalanx of second digit, lateral or outer view; 2, the same, anterior view; 3, the same, medial or inner view; 4, the same; posterior view; 5, the same, superior or proximal view; 6, the same, inferior or distal view; 7, second phalanx of second digit, lateral or outer view; 8, the same, anterior view; 9, the same, medial or inner view; 10, the same, posterior view; 11, the same, superior or proximal view; 12, the same, distal view; 13, distal phalanx of second digit, anterior view; 14, the same, posterior view; 15, the same, proximal view; 16, proximal phalanx of third digit, lateral or outer view; 17, the same, anterior view; 18, the same, inner or medial view; 19, the same, posterior view; 20, the same, proximal view; 21, the same, distal view; 22, second phalanx of third digit, lateral or outer view; 23, the same, anterior view; 24, the same, inner or medial view; 25, the same, posterior view; 26, the same, proximal view; 27, the same, distal end; 28, distal phalanx of third digit, anterior view; 29, the same, posterior view; 30, the same, proximal view.



PHALANGES OF LEFT SECOND, THIRD, AND FOURTH DIGITS
REFERRED BY MARSH TO BRONTOTHERIUM GIGAS

SKELETONS OF MEGACEROPS ACER, MALE AND FEMALE

Mounted in the Colorado Museum of Natural History, Denver, by J. D. Figgins, Director. Photograph furnished by courtesy of Mr. Figgins. Height of male to top of dorsal spine, 1,759 millimeters. One twenty-fifth natural size

APPENDIX

EOCENE AND OLIGOCENE TITANOTHERES OF MONGOLIA

BY

HENRY FAIRFIELD OSBORN

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EOCENE AND OLIGOCENE TITANOTHERES OF MONGOLIA

By Henry Fairfield Osborn

The Eocene and Oligocene titanotheres of Mongolia, discovered in the years 1922 and 1923, after the manuscript of this monograph had been completed and sent to the Geological Survey, are described and figured in this appendix. The outstanding features of the Tertiary formations in which they occur are also described and figured. The appendix closes with a special bibliography relating to the Tertiary of Mongolia and its fauna, so far as it had been described up to the end of the year 1925.

HISTORY OF THEORY AND OF EXPLORATION

ASIATIC CENTERS OF ORIGIN OF MAMMALS

The third Asiatic expedition of the American Museum of Natural History started in 1921 to prepare for its exploration of the Gobi Desert of Mongolia and to test the theory advanced in the year 1900 by the writer of the present monograph that the high plateau region of central Asia would prove to be the arena of the evolution and adaptive radiation of 13 of the principal orders of mammals. This theory was set forth by the writer before the New York Academy of Sciences in two presidential addresses in the years 1899 and 1900 [69] and was graphically illustrated by a world chart (fig. 761) on which the names of 21 orders of placental mammals were printed, together with the places of their origin and distribution according to this theory.

In the text and figures of these addresses the chief continental centers of origin of these orders of mammals appeared as follows:

Africa:
- Proboscidea (elephants and mastodonts).
- Hyracoidea (rock conies).
- Sirenia (manatees and dugongs).

Madagascar:
- Lemuroidea (lemurs).

Oceania:
- Cetacea:
  - Archaeoceti (primitive whales).
  - Mystacoceti (whalebone whales).
  - Odontoceti (toothed whales).

Central Asia:
- Insectivora (insectivores).
- Cheiroptera (bats).
- Creodonta (primitive carnivores).
- Carnivora (modern carnivores).
- Tillodontia (tillodonts).
- Rodentia (rodents).
- Taeniodonta (primitive edentates).

Central Asia—Continued.
- Primates (Mesodonta).
- Amblypoda (Coryphodon and Dinoceras).
- Condylarthra (condylarth ungulates).
- Perissodactyla (odd-toed ungulates).
- Ancylopoda (clawed perissodactyls).
- Artiodactyla (even-toed ungulates).

India:
- Anthropoidea (primates).

South America:
- Edentata (edentates).
- Litopterna (cursorial ungulates).
- Toxodontia (toxodont ungulates).
- Typotheria (typotheres).

Osborn (1900.187, pp. 55, 56) observed:

> Until the Pleistocene, northern Asia is unknown paleontologically—here is a region for explorers; we may consider it as part of a broad Eurasiatic land area extending from the Rocky Mountain region to Great Britain. Every year's discovery increases the resemblances and diminishes the differences between Europe and the Rocky Mountain region. In the absence of all knowledge of Asia, we find the pure or autochthonous fauna of the holarctic region distributed in western Europe and in western North America.

C. W. Andrews (Osborn, 1901–1923) says:

> The above chart of 1900 has been verified by the discovery (1901–1904) of numerous ancestors of the orders Sirenia, Proboscidea, Hyracoidea, Primates, and Archaeoceti in North Africa; more recently (1922, 1923) in central Asia by the discovery of members of the orders Insectivora, Tillodontia, Carnivora, Rodentia, Amblypoda, Perissodactyla, Ancylopoda, and Artiodactyla.

Osborn, in 1925, added: "Charles W. Andrews's discoveries (1901–1904) demonstrate that the primitive whales (Archaeoceti) originated in northern Africa. Osborn is now inclined to place the origin of the Anthropoidea (Primates) in central Asia."

EXPLORATIONS IN MONGOLIA

During the seasons of 1922 and 1923 the third Asiatic expedition, under the leadership of Roy Chapman Andrews, discovered 10 geologic formations of Tertiary age, which contained altogether a very large number of fossil mammals. Part of the territory Andrews explored in 1922 had been crossed by Raphael Pumpelly in 1862–1865; by Obruchev in 1892–1894, who applied the name "Gobi series" to the later sediments; and by Chernov in 1908. Similar territory farther south had been crossed by Von Richthofen in 1877, and it was he who gave the name Khan-Khai beds to the Tertiary sediments he found in the desert region. The underlying series as developed in China,

[69] Osborn, H. F., Science, April, 1900, p. 567.

from the Jurassic downward, had been described by Von Richthofen and later by Bailey Willis in his "Researches in China" (1907).

The geologic personnel of the third Asiatic expedition included Charles P. Berkey as chief geologist, Frederick K. Morris as geologist and topographer, and Walter Granger as vertebrate paleontologist. The party under Andrews consisted of 25 persons—8 Americans, 8 Chinese, and 9 Mongolians.

A single mammalian tooth found by Obruchev in the Iren Dabasu Basin (Houldjin? formation) was identified by the Vienna Museum as a rhinocerid; it is probably *Baluchitherium*, which occurs in the Houldjin gravel. The fossils collected by the third Asiatic expedition (1922–23) from the formations of upper Eocene and of lower and middle Oligocene age, the Mongolian formations best known as yet, so far as catalogued, include 406 specimens, distributed among zones and formations as follows:

Baluchitherium grangeri life zone:	
Hsanda Gol formation, upper part (middle Oligocene)	150
Houldjin formation, upper(?) part (middle Oligocene)	8
Brontops gobiensis life zone:	
Ardyn Obo (lower Oligocene)	46
Protitanotherium mongoliense life zone:	
Shara Murun (uppermost Eocene)	77
Protitanotherium grangeri life zone:	
Irdin Manha (upper Eocene)	99
Arshanto (middle? Eocene)	6
Gashato (basal Eocene or upper Cretaceous)	20

ORDERS OF MAMMALS REPRESENTED IN THE COLLECTIONS

The entire Mongolian collections from the 10 Tertiary formations are more or less clearly recognized as belonging to the following orders of mammals:

Insectivora of the primitive family Pantolestidae.

Creodonta, archaic small-brained carnivores, fairly numerous. Hyaenodontidae, Oxyaenidae, Mesonychidae.

Carnivora, modernized large-brained carnivores, less numerous, first appearing in the upper Eocene (Miacidae) and lower and middle Oligocene (Canidae, Viverridae).

Rodentia, modernized types of rodents, extremely numerous in the middle Oligocene.

Amblypoda, archaic small-brained ungulates, very rare, disappearing in the upper Eocene.

FIGURE 761.—World chart of 1900 explaining Osborn's theory of the central Asiatic origin of the thirteen orders of holarctic mammals, which spread westward to Europe and eastward to North America

After Osborn, 1900.182, p. 567, Chart IV.

Artiodactyla, modernized even-toed ungulates, small and rare in the older formations. Tragulina, Helohyidae, Anthracotheriidae.

Ancylopoda, highly specialized clawed ungulates, very rare. Schizotherium in the Ardyn Obo.

Perissodactyla, modernized odd-toed ungulates, very numerous, representing families of Lophiodontidae, of Amynodontidae, of Baluchitheriinae, of Hyracodontidae, and of Brontotheriidae.

Proboscidea, lower Miocene trilophodonts, lower Pleistocene elephants.

FAMILIES ABSENT

Conspicuous by their absence in these Eocene and Oligocene formations of Mongolia are the primitive three-toed horses of the perissodactyl family of the Equidae. The rôle of these small, swift, cursorial quadrupeds seems to have been taken in upper

Eocene time by the agile lophiodonts of the family Lophiodontidae. The tapirs (Tapiridae) are also absent; these forest-living animals are rare in all flood-plain formations.

CARNIVORA

True Carnivora are first known in the upper Eocene (Miacidae). They are found also in the middle and lower Oligocene (Canidae, Viverridae). The rhinoceroses are represented by three families, members of all of which are rather rare—first, the amphibious Amynodontidae; second, the small, swift, cursorial Hyracodontidae; third, the large, tall, and slender-limbed Baluchitheriinae.

TITANOTHERES

The titanothere family (Brontotheriidae) flourished in upper Eocene time and was the dominant element in the Mongolian fauna. The titanotheres were extremely numerous in Mongolia during the deposition of the upper Eocene Irdin Manha and Shara Murun formations. They also appear in the lower Oligocene Ardyn Obo formation and then apparently disappear. The Oligocene formations Hsanda Gol and Houldjin contain no trace of titanotheres. The dominating hoofed mammals of the middle Oligocene are the great baluchitheres, of the species *Baluchitherium grangeri*. The upper Eocene titanotheres are as large as the existing rhinoceroses, fully twice the size of their American Eocene relatives. Three titanothere life zones have been discovered in the flood-plain formations, known as the Irdin Manha, Shara Murun, and Ardyn Obo; they correspond, respectively, to our Bridger (upper part) and Uinta formations (Eocene) of Wyoming and Utah and the White River group (Oligocene) of Wyoming and South Dakota.

OLDER FORMATIONS

Below these formations is the little-known Arshanto formation, of middle (?) Eocene age, and far below is the Gashato formation, of basal Eocene or Upper Cretaceous age. Above the Ardyn Obo there have been discovered the Houldjin and Hsanda Gol formations, very rich in fossil mammalian life, probably representing lower and middle Oligocene time.

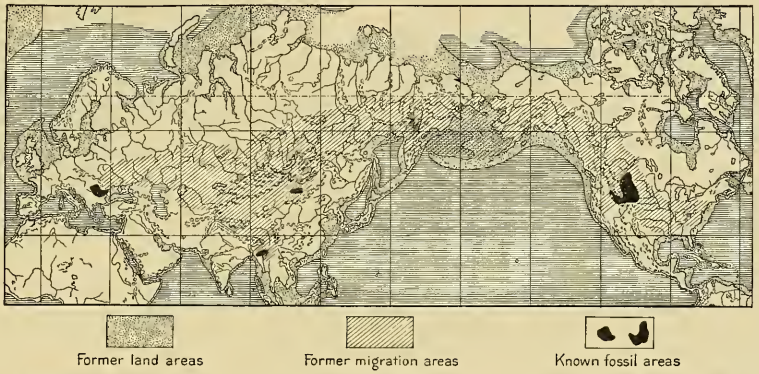


FIGURE 762.—Chief centers of the known zoogeographic distribution of the titanotheres

Rocky Mountain region; Balkan region; Burma region; Gobi Desert of Mongolia.

THE TERTIARY FORMATIONS OF MONGOLIA AND THEIR FAUNAS

NAMES, NAMES OF SUBDIVISIONS, AND THICKNESS

The oldest name applied to the continental sedimentary deposits of the Gobi Basin is the Khan-Khai of Von Richthofen, who used it (1877) with the significance of "deposits of an evaporating sea." No one of these deposits, however, is caused by evaporation; all are strictly continental in origin, and for this reason Obruchev's term Gobi series (1892–1894) is preferable. Gobi means desert basin, and Gobi series is a suitable name for these scattered desert-basin deposits. The name Gobi series was used by Obruchev to include the whole series of late sedimentary beds, without distinction as to age. Obruchev's term is therefore chosen, although Von Richthofen's has priority.

Some of these continental formations may overlap in time, so that the sum of all the thicknesses may not afford an accurate statement of the total column. Making all due allowance, however, for possible overlap, no less than 6,000 to 8,000 feet of Tertiary sedimentary strata have thus far been discovered (1922, 1923) above the post-Jurassic unconformity in the Gobi Desert of Mongolia.

FIGURE 763.—Map of eastern and central Asia showing (3, 4) the area of central Mongolia explored by the American Museum Asiatic expedition of 1922 and 1923. After Osborn, May 25, 1923, p. 2, fig. 1

Within the four circles shown are the middle Oligocene exposures of southern and central Asia in which remains of the giant hornless rhinoceros *Baluchitherium* have been discovered: 1, Bugti beds of Baluchistan, yielding the type of *Baluchitherium osborni;* 2, *Indricotherium* (= *Baluchitherium*) zone of Turgai, northern Turkestan; 3, *Baluchitherium grangeri* zone (Houldjin formation), southeastern Mongolia; 4, *Baluchitherium grangeri* type zone (Hsanda Gol formation), central Mongolia. Upper Eocene and lower Oligocene titanotheres occur near area 3. Certain upper Eocene species of titanotheres and of amynodonts are also found in Burma along Irrawaddy River.

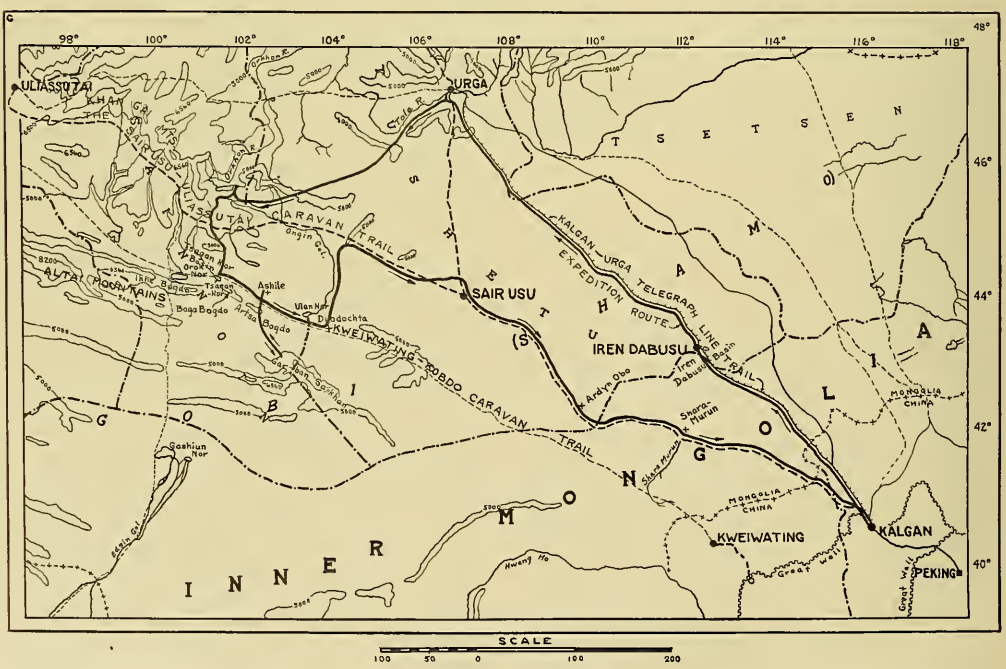


FIGURE 764.—Route map of the American Museum expedition of 1922 and 1923 in southeastern and central Mongolia, showing the three localities where titanotheres were discovered. After Berkey and Granger, May 25, 1923, p. 2, fig. 1

The three localities are the Iren Dabasu Basin, in which lies the Irdin Manha formation (*Protitanotherium grangeri* zone), upper Eocene, on the Kalgan-Urga trail; Shara Murun (*Protitanotherium mongoliense* zone), uppermost Eocene, on the Kalgan-Sair Usu-Uliassutai trail; and Ardyn Obo (*Brontops gobiensis* zone), lower Oligocene, on the Kalgan-Sair Usu-Uliassutai trail. These and other fossil fields are indicated by local Mongol names employed to designate the respective formations.

In the seasons of 1922 and 1923 the third Asiatic expedition discovered 10 Tertiary formations within the Gobi series as designated by Obruchev. These formations are more or less clearly recognizable and correlated with those of Europe, Asia, and North America by the fossils they contain, as follows:

Tertiary formations of Mongolia, in descending order

Formation	Estimated thickness in feet	Geographic region	Life zone	Probable or estimated age	American correlation equivalent
Hung Kureh	2,000	Eastern Altai	Hipparion, Camelus? zone	Upper Pliocene or lower Pleistocene.	
Pang Kiang	500	Iren Dabasu Basin		Pliocene?; age very doubtful.	
Loh	100–1,000	Eastern Altai	Serridentinus (Trilophodon) mongoliensis zone.	Lower Miocene	
Hsanda Gol	3,000	do	Baluchitherium grangeri zone.	Lower and middle Oligocene.	Oreodon and Metamynodon.
Houldjin	30	Iren Dabasu Basin	Baluchitherium grangeri? zone.	do	
Ardyn Obo	500	Uliassutai trail	Titanothere life zones: Brontops gobiensis zone.	Lower Oligocene. Last? appearance of titanotheres.	White River group, Chadron formation.
Shara Murun	500	do	Protitanotherium mongoliense zone.	Summit of Eocene. Titanotheres very abundant.	Uinta formation (Diplacodon zone).
Irdin Manha	40–100	Iren Dabasu Basin	Protitanotherium grangeri zone.	Upper Eocene. Titanotheres present.	Bridger formation (Eobasileus zone), horizon B of Uinta Basin.
Arshanto	40–100	do	Lophiodont-Schlosseria zone.	Middle? Eocene	Bridger formation(?).
Gashato	300	Eastern Altai	Palaeostylops iturus zone	Basal Eocene or Upper Cretaceous.	Possibly Puerco, Torrejon, or Fort Union formation of the Eocene.
	7,150				

PLIOCENE OR PLEISTOCENE: HUNG KUREH FORMATION

Berkey and Granger (May 25, 1923, p. 9)

Thickness.—The sub-Altai Hung Kureh formation, named after the hills of Hung Kureh, measuring in thickness approximately 2,000 feet, rests conformably upon the Hsanda Gol formation and is marked above by Pleistocene erosion. It lies in the very bottom of the basin of Tsagan Nor, between the foot of the mountain of Baga Bogdo and the Tsagan Nor itself, and consists of a series of gravelly sands and conglomerates of great variety and thickness, at the base of which lie whitish and yellowish sands and clayey sands. Although the formation is not so well exposed as the Hsanda Gol, it has been possible to measure more than 1,000 feet of it, and a reasonable estimate of its total thickness in the type locality—the hills of Hung Kureh—is 2,000 feet. On its extreme margin next to the mountain of Baga Bogdo the upper beds

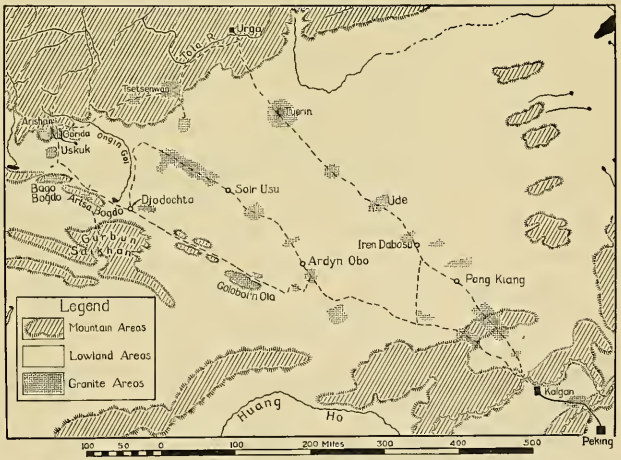


FIGURE 765.—Map of central Mongolia (Gobi Desert region), traversed by the third Asiatic expedition, Roy Chapman Andrews, leader

Dotted lines show main routes and location of the chief Cretaceous and Tertiary exposures: Iren Dabasu (Upper Cretaceous), north of Irdin Manha (Tertiary, upper Eocene), Pang Kiang (Tertiary, Miocene?) Ardyn Obo (Tertiary, lower Oligocene), and Djadochta (Lower Cretaceous, *Protoceratops* zone). This area includes about 475,600 square miles and lies northwest of Kalgan and Peking. After Berkey and Morris, The great bathylith of central Mongolia, p. 2, fig. 1, 1924.

become a coarse conglomerate, and the influence of this rising mountain is shown by alluvial conglomeratic fans.

Fauna.—These massive Hung Kureh beds are fossiliferous only at their base. Here and there a bed does carry fossils, particularly in the lowermost part of the formation, within 200 or 300 feet of its base, where deposits of yellow iron-stained sand and beds of white sand prevail. The fossil content of the lower Hung Kureh as first identified in the field and in the American Museum is as follows: A few fragments of a Pliocene horse [*Hipparion* sp.]; a few bones and fragments of shells of the eggs of a very large bird, probably *Struthiolithus*; a large cervid [*Cervus* sp.?]; a proboscidean; a rhinoceros; a camel-oid; a rodent [*Castor*]. This fauna indicates an uppermost Pliocene or lowermost Pleistocene age.

PLIOCENE?: PANG KIANG FORMATION

Granger, Berkey, and Morris (October 7, 1924, p. 119)

About 60 miles southeast of Irdin Manha are the Pang Kiang beds, about 500 feet thick, provisionally placed in the Pliocene. In some places at least these beds rest directly upon old crystalline rocks. Only one fossil has been found in the Pang Kiang, a fragment of the jaw of a rodent which Matthew identifies as an ochotonid of more recent age than Oligocene. The rodent family Ochotonidae first appears in the middle Oligocene of Europe and much more recently in the Pleistocene of North America as the pika, or mountain hare.

FIGURE 766.—Map and section of the eastern Altai region, showing location of the Tertiary formations

Hung Kureh, of Pliocene or Pleistocene age; Loh, of lower Miocene age; Hsanda Gol, of middle and lower Oligocene age; Gashato, of basal Eocene or Upper Cretaceous age After Berkey and Morris, Basin structures in Mongolia, figs. 9 and 10, 1924.

Approximate position of ten Mongolian formations in the geologic column, as determined to the year 1924 by the fossiliferous levels only

[Thick formations or series like the Hsanda Gol and Hung Kureh doubtless occupy a larger part of the column. A query (?) indicates that the level is determined only provisionally]

		Feet
Pleistocene	(?) Hung Kureh	2,000
Pliocene	(?) Pang Kiang	500
Miocene	Loh	100–1,000
Oligocene	(?) Hsanda Gol	3,000
	(?) Houldjin	30
	Ardyn Obo	500
Eocene	Shara Murun	500
	Irdin Manha	40–100
	(?) Arshanto	40–100
Upper Cretaceous	(?) Gashato	300

MIOCENE: LOH FORMATION

Granger, Berkey, and Morris (October 7, 1924, p. 115)

Definition.—The Loh formation was first defined as follows:

The lower Miocene clays of Loh, less than 100 feet thick, resting upon the Hsanda Gol clays, without any obvious physical disconformity. Going southward along their dip (fig. 10), we found that they were succeeded by an undetermined thickness, probably as much as 1,000 feet, of sandy clays and sands, in which as yet no fossils have been found.

Osborn added (November 11, 1924, p. 1):

In a thin deposit of olive-colored clays and light-gray sandstone resting on the red-banded beds of the Hsanda Gol formation at Loh, and believed to be of lower Miocene age, were found two highly characteristic fossils: (1) Proboscidean. A fragmentary series of lower mastodont teeth (Am. Mus. 19152) which first reveals the presence of an undoubted *Serridentinus* in Mongolia, which we name *Serridentinus mongoliensis*. *Serridentinus* probably marks the arrival of a proboscidean related to the *M.* [*Trilophodon*] *angustidens* of the lower Miocene of Europe. * * * (2) Rhinocerotine. The facial portion of a skull (Am. Mus. 19185) containing three grinding teeth and perfectly preserved nasals, which we name *Baluchitherium mongoliense*.

Fauna.—The type of *Serridentinus* (*Trilophodon*) *mongoliensis* is a smaller and more primitive trilophodont mastodon than its successor *Serridentinus productus* of the upper Miocene marls (lower part of Santa Fe formation) of New Mexico. Its ancestors are found in Miocene lignitic deposits of western Europe, its descendants in Pliocene deposits of Texas and Florida. The type of *Baluchitherium mongoliense* indicates a hornless rhinoceros little more than half the size of the type of *Baluchitherium grangeri* of the Hsanda Gol, but with premolar teeth of a more progressive stage. These two fossils from the Loh formation, *Serridentinus* (*Trilophodon*) *mongoliensis* and *Baluchitherium mongoliense*, confirm the judgment of Granger, Berkey, and Morris as to the probable lower Miocene age of the Loh formation.

OLIGOCENE: HSANDA GOL FORMATION

Berkey and Granger (May 25, 1923, p. 8)

Stratigraphic position and lithologic character.—The fine series of Tertiary deposits called the Hsanda Gol formation, so far as discovered up to 1923, lies unconformably upon the unevenly eroded surface of the Ondai Sair formation, of Lower Cretaceous (Comanche) age. Prevailingly yellowish conglomerates and pebbly sands, varying greatly in quality, constitute at least 800 feet of the lowermost beds; the middle beds consist of alternating sands, marls, clays, and clayey sands of variegated colors, chiefly red, yellow, and white, with no apparent uniformity of succession; the uppermost beds [fossiliferous] are prevailingly sands and clayey sands, are reddish in color, and include some beds that are fairly well indurated.

This whole series of beds stretches along the Hsanda Gol, a dry, sandy stream course leading from Mount Uskuk through the Ondai Sair locality southward past Loh to the bottom of the basin of Tsagan Nor, at the foot of Baga Bogdo, a total distance of about 15 miles. Altogether, a thickness of approximately 3,000 feet of the formation has been measured and estimated from measurements, and a large part of it has been inspected in detail.

The uppermost beds of the formation are fossiliferous, the middle beds are largely barren, and no fossils whatever are found in the lowermost beds. In the middle beds a fossil is found here and there, but fossils are numerous in the uppermost beds only. These uppermost beds are judged to be of Miocene [Oligocene] age, but whether the whole thickness of 3,000 feet to the underlying Cretaceous is also Miocene [Oligocene] is not known; yet in the absence of any physical break in the whole Hsanda Gol formation, it is regarded as a unit of Miocene [Oligocene] age. Thousands of fossils, chiefly rodents, were collected from the uppermost beds, especially in the vicinity of Loh, 10 miles downstream from Ondai Sair, and near the so-called Grand Gorge, a corresponding erosion exposure 10 miles farther west.

Fauna (1923–1925).—Originally regarded by Berkey and Granger (1923) "as a unit of Miocene age," the fossiliferous uppermost levels [sands and clayey sands] of the Hsanda Gol are now known to be of middle Oligocene age, but it is believed that the formation may well extend down at the base to upper Eocene.

Matthew and Granger (January 18, 1924, p. 5) listed 22 genera and 26 species of Insectivora, Creodonta, Carnivora, Rodentia, Perissodactyla, and Artiodactyla of the Hsanda Gol formation. Both the Creodonta and the Carnivora are in an Oligocene stage of evolution tending to early Oligocene; the Rodentia appear to be of lower and middle Oligocene age; the

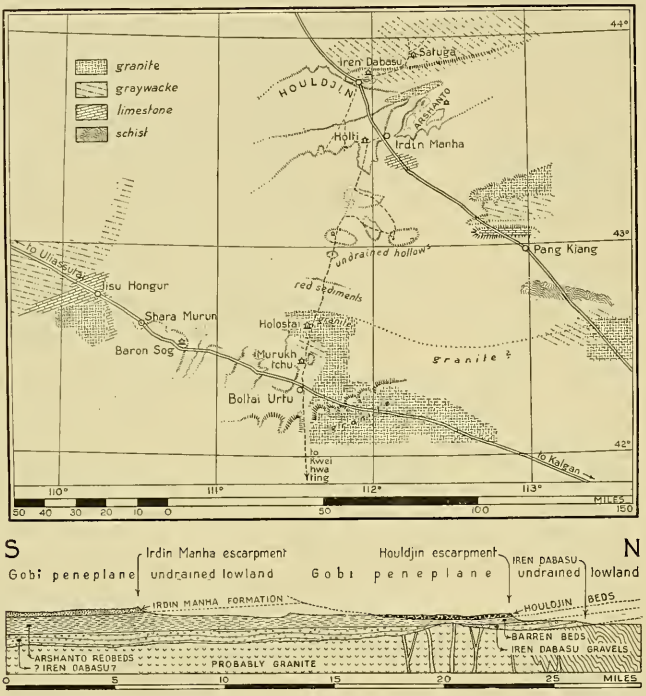


FIGURE 767.—Map and section of the east-central Gobi Desert, showing location of the chief Cretaceous and Tertiary formations discovered in this region

Iren Dabasu (Upper Cretaceous dinosaur beds), Houldjin (contains middle Oligocene *Baluchitherium* zone), Irdin Manha (upper Eocene *Protitanotherium grangeri* zone), Arsbanto (middle (?) Eocene lophiodont-*Schlosseria* zone), Pang Kiang (Miocene?), Shara Murun (uppermost Eocene *Protitanotherium mongoliense* zone). The section shows the Irdin Manha formation (upper Eocene) overlying the Arshanto red beds (middle (?) Eocene), which in turn may overlie the Iren Dabasu (Upper Cretaceous dinosaur beds); also the Houldjin formation (middle and lower Oligocene) apparently overlying the Arsbanto red beds (middle (?) Eocene). After Berkey and Morris, Basin structures in Mongolia, figs. 12, 13, 1924.

The forms taken from the uppermost beds include (op. cit., p. 9) "*Baluchitherium*, a fine skull nearly 5 feet long [*Baluchitherium grangeri*], and other rhinocerids; rodents by the hundreds; artiodactyls; insectivores; and carnivores." The fossiliferous uppermost beds of this formation or series are termed the *Baluchitherium grangeri* zone.

Insectivora also appear to be of Oligocene age; one artiodactyl, comparable to certain artiodactyls of the French Oligocene Phosphorites, is a true primitive cervid, *Eumeryx*. In the perissodactyl hornless rhinoceros *Baluchitherium grangeri* the premolar evolution is more modernized or recent than that of the *Indricotherium asiaticum* Borissiak of Turgai, Turkestan.

Preliminary lists of middle (?) and upper Eocene and Oligocene Mongolian fossil faunas as determined to June 30, 1925, by Osborn, Matthew, and Granger

Order and family	Middle Eocene: Arshanto formation	Upper Eocene		Lower Oligocene: Ardyn Obo formation	Middle Oligocene: Upper part of Hsanda Gol and Houldjin formations
		Irdin Manha formation	Shara Murun formation		
Creodonta:					
Mesonychidae		Andrewsarchus, ?Harpagolestes, ?Synoplotherium, ?Hapalodectes.	Olsenia mira		
Hyaenodontidae		Hyaenodon irdinensis.	Pterodon hyaenoides	Hyaenodon eminus	Hyaenodon and 2 genera.
Oxyaenidae				Ardynictis furunculus.	
Carnivora:					
Canidae, Miacidae, Viverridae.		Miacis invictus		Cynodictis	Amphicticeps and 3 genera.
Rodentia		?Paramys	?Desmatolagus	Desmatolagus	9 genera, 11 species.
Amblypoda		Eudinoceras mongoliensis.			
Artiodactyla:					
Tragulina			Archaeomeryx	Lophiomeryx, (2 species), Miomeryx.	Eumeryx culminis.
Helohyidae		Gobiohyus			
Anthracotheriidae		Genus indet		?Ancodon	
Entelodontidae					Entelodon dirus.
Perissodactyla:					
Lophiodontidae	Schlosseria	Teleolophus, Desmatotherium mongoliense, D. fissum.	Deperetella cristata	Colodon inceptus, Paracolodon curtus.	
Rhinocerotoidea:					
Hyracodontidae	Teilhardia	Caenolophus (1 species), Lophialetes.	Caenolophus (4 species).	Ardynia praecox	
Amynodontidae		?Amynodon	Amynodon (or new genus).	Cadurcotherium ardynense.	
Rhinocerotidae—Baluchitheriinae.			Baluchitherium (or new genus).		Baluchitherium grangeri.
Titanotheroidea:					
Brontotheriidae		Protitanotherium grangeri, Telmatherium berkeyi, Dolichorhinus olseni, Manteoceras? mongoliensis, Metarhinus? mongoliensis.	Protitanotherium mongoliense, P. andrewsi, Dolichorhinus kaiseni.	Brontops gobiensis, Menodus mongoliensis.	
Chalicotheriidae				Schizotherium avitum	

OLIGOCENE: HOULDJIN FORMATION

Granger and Berkey (August 7, 1922, p. 4)

The type locality of the Houldjin formation is 5 miles south of Iren Dabasu. It consists of sand and gravel, 30 feet in total thickness; with a coarse sandy conglomeratic member at base (5 feet), fossiliferous. Originally characterized by the following fossil content: (1) A rhinocerid [?*Caenopus* or *Praeceratherium* sp., ?*Cadurcotherium* sp.]; (2) a large carnivore [*Entelodon dirus*, equal in size to *Dinohyus hollandi*, lower Miocene of Nebraska]; (3) an artiodactyl of the size of a Virginia deer [?*Entelodon* sp.]; (4) an enormous mammal, possibly related to or identical with *Baluchitherium* of Baluchistan [?*Baluchitherium*]; (5) a tortoise of large size [?*Testudo*].

It was from the Houldjin gravel, probably, that Obruchev obtained the rhinocerid molar tooth (?*Baluchitherium*) The Houldjin was regarded by Granger and Berkey (1922, p. 4) as of more recent age than the underlying Irdin Manha formation and as equivalent in age to the Hsanda Gol formation, because both contain *Baluchitherium*.

In 1923 Matthew and Granger (December 18, pp. 1–6) described the fragmentary Houldjin fossils indicated above in brackets, also those given in the accompanying table. They concluded in general that this fauna is of Oligocene age but can not be exactly correlated until better known; it may be homotaxic with the Hsanda Gol fauna, but this supposition rests only on the doubtfully identified *Baluchitherium;* the Houldjin and Hsanda Gol type localities are more than a thousand miles apart, and the geologic character of the two formations is quite different. The amynodont ?*Cadurcotherium* is comparable with that of the Ardyn Obo formation, *Cadurcotherium ardynense* Osborn. The large *Baluchitherium* is comparable with that from Turgai described by Borissiak. The smaller rhinocerid is comparable in size with *Caenopus occidentalis*, from the Oligocene of Nebraska, with the *Epiaceratherium turgaicum* Borissiak of Turgai, and with the *Aceratherium filholi* Osborn of the Phosphorites, Oligocene; its relationships remain to be determined.

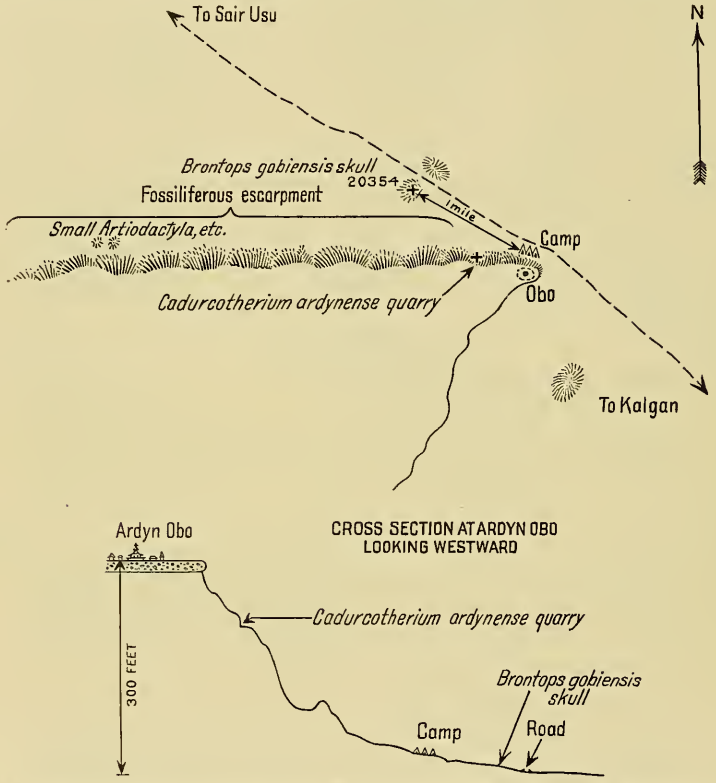


FIGURE 768.—Ardyn Obo formation (lower Oligocene), after field notes and sketches by Granger

Upper part: Sketch map of Ardyn Obo formation, showing location of the principal finds, namely, type skull of *Brontops gobiensis* (Am. Mus. 20354), *Cadurcotherium ardynense* quarry, and small Artiodactyla.
Lower part: Cross section of the Ardyn Obo formation, showing the levels on which the remains of *Cadurcotherium ardynense*, *Brontops gobiensis*, and *Menodus mongoliensis* were found.

LOWER OLIGOCENE: ARDYN OBO FORMATION

Berkey and Granger (May 25, 1923, p. 12)

Type locality and notable features.—The type locality of the Ardyn Obo formation on the main Kalgan-Uliassutai trail is south of Sair Usu, where a great escarpment, surmounted by an obo (the inevitable guidepost of the Mongolian desert), stands 300 feet above the general level of the plain over which the Uliassutai trail passes, and where for many miles the

edges of the flat-lying strata are exposed. These strata are formed of rather loose and slightly indurated sandstone and clayey sand of considerable variety of texture, quality, and color. In the upper members of the Ardyn Obo formation fossils were obtained, including several fine specimens of rhinocerids and numerous fragments of turtles. Although it is judged to be of mid-Tertiary age, the Ardyn Obo can not be correlated with either the Hsanda Gol or the Houldjin formation.

Morris and Granger (notes, 1925) report as follows:

On top of the Ardyn Obo beds lies a heavy sandstone capping, which has preserved at its present level this great mesa. The beds are predominantly sandy but include some layers of shale. The fossils were collected along the face of the great Ardyn Obo bluff and at its base, about 300 feet from the summit sandstone capping; the remaining 200 feet lies out in the basin and is not well exposed. The *Cadurcotherium ardynense* quarry, opened in 1922 and again worked in 1923, was within 100 feet of the top of the mesa, and most of the teeth and bones of this small aquatic rhinoceros came from about this level. The numerous artiodactyl jaws, accompanied by an occasional rodent or carnivore, were found on knolls at the base of the great bluff, 150 and 200 feet below its top. The skull of the titanothere *Brontops gobiensis* was found at the lowest collecting level, about 300 feet below the top of the sandstone capping.

Fauna.—Matthew and Granger (December 18, 1923, pp. 1–5) described the small collection of mammals obtained in 1922 at "Promontory Bluff," on the Sair Usu-Kalgan trail, about 150 miles from Sair Usu and 350 from Kalgan. They concluded that this appears to be an Oligocene fauna; *Cadurcotherium*, *Schizotherium*, and *Cynodictis* are generically characteristic of the Phosphorites of Quercy; a giant tortoise (*Testudo insolitus*) is apparently in a rather primitive stage. The nearest zoogeographic affinities of this fauna are with western Europe rather than with the western United States.

Osborn (1925) added the important titanothere genus and species *Brontops gobiensis*, which relates this formation to the lower Oligocene of South Dakota.

FIGURE 769.—Ardyn Obo formation (lower Oligocene) of Mongolia, where the types of *Brontops gobiensis* and *Cadurcotherium ardynense* were discovered

American Museum camp of 1923 in the foreground. After Am. Mus. negative No. 251603.

Brontops gobiensis life zone.—The name "*Brontops gobiensis* life zone" has been assigned by Osborn to the Ardyn Obo formation to emphasize the fact that *Brontops gobiensis* is strikingly close in its evolution to *Brontops brachycephalus* and to *Teleodus avus*, discovered in the lower *Titanotherium* life zone (Chadron formation) in the great Badlands of South Dakota. This robust, broad-headed little titanothere was discovered some 300 feet below the top of the Ardyn Obo formation, which is altogether over 500 feet in thickness as measured by Morris. We may confidently assign a lower Oligocene age to this formation. A single lower molar represents

Menodus mongoliensis, a much larger animal than *Brontops*, characteristic of a higher geologic level.

Osborn (October 19, 1923) described *Cadurcotherium ardynense* as resembling *Cadurcotherium cayluxi* of the Oligocene Phosphorites of France. The quarry containing these rhinoceroses (*Cadurcotherium ardynense*) lies 200 feet above the *Brontops gobiensis* level, or 100 feet below the top of the mesa, which is protected by a heavy sandstone capping that preserves it from erosion.

SUMMIT OF THE EOCENE: SHARA MURUN FORMATION

Berkey and Granger (May 25, 1923, p. 12)

General features.—A hundred miles south of the Ardyn Obo formation is a distinct basin carrying fossiliferous strata which have been called the Shara Murun formation. The sedimentary area is very large and the best exposures occur along the borders of a 200-foot escarpment. At this place were found titanothere remains resembling those found in the Irdin Manha formation early in the season of 1922. These beds are assigned a total thickness of 500 feet.

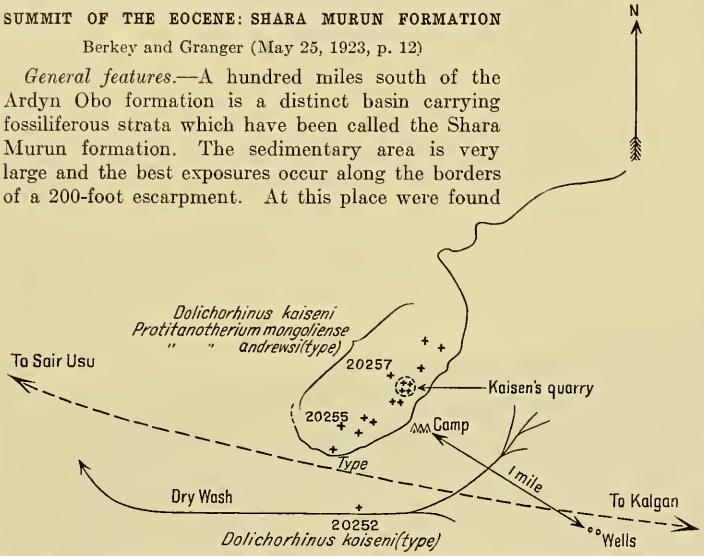


FIGURE 770.—Field sketch of the chief fossiliferous beds of the Shara Murun formation near Ula Usu, on the Kalgan-Uliassutai trail, showing where the types of *Protitanotherium andrewsi*, *P. mongoliense*, and *Dolichorhinus kaiseni* were discovered

Unlike the Irdin Manha quarries, the fossiliferous localities are close together in the Shara Murun formation. After sketch by Walter Granger, chief paleontologist of the third Asiatic expedition.

The first fossil found in this formation was a titanothere, which Osborn (October 17, 1923, p. 3) identified as *Protitanotherium mongoliense*, a form closely intermediate in size and characters between *Protitanotherium emarginatum* and the large *Protitanotherium superbum*, both of the Uinta formation (horizon C of Uinta Basin) of northern Utah (compare fig. 778).

According to Granger a total thickness of over 300 feet is exposed at this type locality. The fossils are distributed through a vertical thickness of about 150 feet; this may account for the presence in the upper levels of *Protitanotherium andrewsi*, a more progressive species than *Protitanotherium mongoliense*, which, in turn, is much more progressive than the species *Protitanotherium grangeri* of the Irdin Manha formation. The Shara Murun beds near Ula Usu have somewhat the appearance of those of the Irdin Manha formation at the Irdin Manha bench—gray shales above and red shales at the base—but they weather out in deeper gulches. Calcareous concretions are rare in the 150 feet of rich fossiliferous beds. There is much local slipping of the clays, whereby many of the titanothere crania were badly crushed and distorted, so that they required careful restoration. The titanothere bones of the Shara Murun are readily distinguishable by their light cream color and softer texture from the rust-brown bones found in the Irdin Manha.

Fauna.—The fauna of the Shara Murun formation is more recent than that of the Irdin Manha. The small lophiodonts (*Desmatotherium*) that swarm in the Irdin Manha are rare in the Shara Murun, which carries many larger lophiodonts (*Deperetella*) and long-limbed baluchitherine (?) rhinoceroses (ancestral *Baluchitherium?*), as well as numerous *Amynodon*. The great herds of lophiodonts found in the Irdin Manha are replaced in the Shara Murun by small traguline artiodactyls. These artiodactyls (*Archaeomeryx*) were found in layers that contained no other mammals and may represent small herds suddenly overcome. The large lophiodonts (*Deperetella*) were also found by themselves, many individuals compacted in a small area.

The rhinoceroses, which are rare in the Irdin Manha, are fairly abundant in the Shara Murun and are at some places mingled with titanotheres but are generally segregated. They include one complete skeleton of *Amynodon* in a stage of evolution similar to that of *Amynodon antiquus* of the upper part of the Bridger formation (horizon B of Uinta Basin) of Utah. Skeletal remains and jaws and teeth of five very long-limbed baluchitherine (?) rhinoceroses were found, which may prove to be ancestral to the *Baluchitherium grangeri* of the middle Oligocene.

The titanotheres of the three species *Dolichorhinus kaiseni*, *Protitanotherium mongoliense*, and *Protitanotherium andrewsi* dominate all other mammals, and in one quarry (fig. 770) a large deposit of these bones was found and worked by Kaisen during June and September, 1923. In the Shara Murun, as in the upper Eocene "*Titanotherium* beds" of the Rocky

Mountains, some of the skulls include jaws, but few are found associated with parts of the postcranial skeleton. Only one fairly complete skeleton of a titanothere was found in the Shara Murun, a specimen that had been in part destroyed by the weather. This skeleton bears the number Am. Mus. 20277. Incomplete limb and foot bones of six other skeletons were also collected. All the 17 or more specimens of titanotheres collected, except one titanothere skull with jaws (Am. Mus. 20252), were found in one rather small area just north of the Kalgan-Uliassutai trail. This area, which has a radius of about a third of a mile, was a veritable bone bed, and the large collection of remains of titanotheres obtained from it represents only a small part of the fossils actually weathered out, a fact that indicates the extreme abundance of these titanotheres in central Mongolia in upper Eocene time.

Protitanotherium mongoliense life zone.—The faunistic name "*Protitanotherium mongoliense* life zone" was given by Osborn to the Shara Murun formation on determining that the species of titanotheres which they contain are considerably more recent in age than those of the Irdin Manha formation. Altogether more than 17 specimens of titanotheres have been found in a single fossiliferous exposure, distributed as follows:

Protitanotherium andrewsi, the most progressive species, represented by the type and six other specimens, also skeletal material, probably belonging in upper levels.

Protitanotherium mongoliense, represented by the type and five other specimens, also skeletal material.

Dolichorhinus kaiseni, represented by the type and three other specimens.

UPPER EOCENE: IRDIN MANHA FORMATION

Granger and Berkey (August 7, 1922, p. 5)

Locality and characteristic features.—About 25 miles south of the Houldjin formation a conspicuous member of Obruchev's Gobi series, called the Irdin Manha formation, immediately overlies the Upper Cretaceous Iren Dabasu formation. It consists of cross-bedded sandstones, limy sand, and pebbly sandstones and comprises a barren upper member (25+ feet thick) and a lower member, the lophiodont-bearing bed (4 feet thick). Originally characterized by (1) small Lophiodonta of at least two species in great abundance [*Desmatotherium*]; (2) a perissodactyl [*Protitanotherium*] about the size of the upper Eocene titanotheres and possibly related to this family; (3) a small artiodactyl [*Gobiohyus*]; (4) a small creodont [*Hyaenodon*]; (5) an abundance of turtles of both the hard-shelled and soft-shelled groups; (6) teleost fishes.

Granger (notes, 1925) reports as follows: The Irdin Manha bench, which extends north and south, is about 22 miles southeast of Iren Dabasu on the Kalgan-Urga trail and about 143 miles north of Kalgan. The fossiliferous outcrop occurs along an escarpment that is several miles long, with a few outlying buttes. The Kalgan-Urga trail and the telegraph line drop down over this escarpment at or near the center of the fossiliferous area. Other small exposures of the Irdin Manha formation, sparingly fossiliferous,

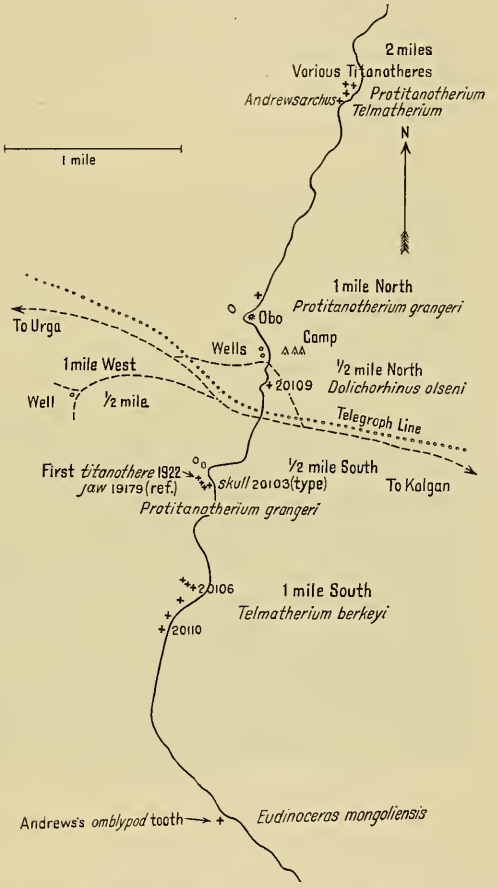


FIGURE 771.—Field sketch map of exposures of the Irdin Manha formation 22 miles southeast of Iren Dabasu, on the Kalgan-Urga telegraph line, showing the chief locations at which collections of titanotheres were made

The points at which fossils were collected extend from 2 miles north to 2 miles south of the telegraph line. The fossils collected are *Protitanotherium grangeri*, *Telmatherium berkeyi*, and *Dolichorhinus olseni;* also the giant creodont *Andrewsarchus* and the first giant amblypod found in Asia, *Eudinoceras*. After sketch by Walter Granger, chief paleontologist of the third Asiatic expedition.

were observed 20 miles west and 20 miles north of the type locality.

Fauna.—The lophiodont of the Irdin Manha beds was named by Osborn (October 17, 1923, p. 2) *Desmatotherium mongoliense*, an animal specifically, if not generically, distinguishable from *Desmatotherium*

guyotii of horizon C? or D of the Bridger formation of Wyoming (middle Eocene). Osborn (November 10, 1924) described as *Eudinoceras mongoliensis* a large upper Eocene amblypod related to the *Dinoceras* of Marsh and to the *Loxolophodon* of Cope, animals surviving to the upper Eocene horizon B of the Uinta Basin of Utah. Osborn also described (November 11, 1924) *Andrewsarchus mongoliensis*, a giant creodont of the family Mesonychidae, which attained its zenith in the upper Eocene (Uinta B horizon) of North America.

Protitanotherium grangeri life zone.—On studying the fauna of the Irdin Manha formation, Osborn (1925) assigned to the formation the name *Protitanotherium grangeri* life zone because of its content of the characteristic mammalian titanothere *Protitanotherium grangeri*. It contains also, however, remains of *Telmatherium berkeyi* and *Dolichorhinus olseni*, as well as of other species. The species *Protitanotherium grangeri* and *Dolichorhinus olseni* are much more primitive than their successors *Protitanotherium mongoliense* and *Dolichorhinus kaiseni* in the Shara Murun formation; consequently the Irdin Manha formation is older than the Shara Murun formation. The Irdin Manha formation has yielded remains of 23 or more titanotheres and chalicotheres. The following list shows the relative abundance of five species:

Protitanotherium grangeri, represented by thirteen skulls and jaws and other skeletal remains.

Telmatherium berkeyi, represented by seven specimens, jaws and teeth.

Dolichorhinus olseni, represented by one specimen, a pair of jaws.

Manteoceras? irdinensis, represented by one jaw; generic reference doubtful.

Metarhinus? mongoliensis, represented by one jaw and two teeth; generic reference doubtful.

By far the most abundant mammal of the Irdin Manha formation is the small lophiodont (*Desmatotherium mongoliense*), represented by innumerable specimens. Next in abundance are the titanotheres. The carnivorous Creodonta, especially the family Mesonychidae, are very common. Of the family Mesonychidae the skull of *Andrewsarchus mongoliensis* is of great size and is well preserved. The rhinoceroses are represented by the Hyracodontidae (*Caenolophus*, *Lophialetes*) and probably by the Amynodontidae (*Amynodon*), both types rare in this formation. All other mammals (artiodactyls, rodents) are rare. The giant amblypod *Eudinoceras mongoliensis* is represented only by two teeth.

FIGURE 772.—Irdin Manha formation (upper Eocene of Mongolia, *Protitanotherium grangeri* zone)

Irdin Manha bluff, looking northward across the Kalgan-Urga trail. After Am. Mus. negative No. 251584, by R. C. Andrews

MIDDLE (?) EOCENE: ARSHANTO FORMATION

Berkey and Morris (October 7, 1924, p. 119)

Locality and lithology.—Twenty miles southeast of Iren Dabasu, in the Irdin Manha Basin, at the base of the Irdin Manha section, is a lower series of red beds to which the name Arshanto is given.

Beneath the titanothere beds [Irdin Manha] there are red clays, provisionally called Arshanto, probably to be correlated

with the barren beds above the Iren Dabasu. The Arshanto may prove to be only the lower Irdin Manha, or it may be separated from the Irdin Manha by a disconformity. The base of these beds has not been seen.

The type locality of the Arshanto formation is 7 miles northeast of the Kalgan-Urga trail. The Arshanto consists of reddish shales, which appear from the latest faunistic evidence to belong to an earlier life zone, distinct from the Irdin Manha or *Protitanotherium grangeri* zone, yielding an abundance of lophiodonts, which are found in the red shales at one point. In the red shales to the north, at Iren Dabasu, beds of the same appearance and presumably of the same age, which overlie the Iren Dabasu Cretaceous, yield a few scraps of lophiodont teeth.

Fauna.—Small perissodactyls are abundant in these beds and are described by Matthew and Granger (1925) as *Schlosseria*, a lophiodont, and *Teilhardia*, originally referred to the primitive rhinoceros family of Hyracodontidae.

BASAL EOCENE OR UPPER CRETACEOUS: GASHATO FORMATION

Berkey and Morris (October 7, 1924, pp. 117, 125)

The Gashato clays and gravels, which are of basal Eocene or Upper Cretaceous age, immediately overlying the Djadochta formation (*Protoceratops* zone), carry an early Eocene fauna, according to field identifications by Granger and careful revision by Matthew and Granger (1925). The known faunal list is as follows:

Palaeostylops iturus. Order Notoungulata (ungulates of the Southern Hemisphere). Notoungulates (*Arctostylops*) have been discovered in Wyoming and in South America.

Prionessus lucifer. Order Multituberculata (=multituberculates); also known in the Cretaceous and basal Eocene of western Europe and of North America.

Baënomys ambiguus. Order Glires; resemblances to both the Simplicidentata and the Lagomorpha.

Eurymylus laticeps. Order Insectivora?, Menotyphla?

Phenacolophus fallax. Order Condylarthra?; archaic pentadactyl ungulates.

Hyracolestes ermineus. Order Creodonta; archaic carnivores.

Sarcodon pygmaeus. Order Insectivora?

The ancestral relationship of the Mongolian *Palaeostylops* to the American *Arctostylops* of our lower Eocene Wasatch formation is indicative of "Paleocene" (basal Eocene, Torrejon) or Upper Cretaceous age. The remaining species of multituberculates, insectivores, rodents, and creodonts show no characters precluding the possibility of "Paleocene" or basal Eocene age, although these species do not represent ancestors of the Eocene faunas of Europe or of North America, as might have been expected. The absence of ancestors to the higher ungulates, perissodactyls, artiodactyls, and like forms points to this Gashato fauna as a surviving archaic fauna of basal Eocene or Upper Cretaceous age.

HISTORY OF THE DISCOVERY OF REMAINS OF TITANOTHERES IN MONGOLIA

Among the first fossils discovered in the Gobi Desert in 1922 was a left lower jaw of a titanothere with six grinding teeth (first premolar to second lower molar), found by Prof. Charles P. Berkey in the Irdin Manha formation on May 4, 1922. To this first titanothere discovered in Mongolia is now assigned the American Museum number 19179 and it is referred to the species *Protitanotherium grangeri*, the type of which was named from another specimen in honor of Walter Granger, chief paleontologist of the expedition.

Recognizing the great importance of this discovery, the leader of the expedition, Roy Chapman Andrews, immediately announced it by cable to the American Museum: "First titanotheres discovered." This first titanothere jaw found in the Irdin Manha formation of Mongolia recalls the fact that Joseph Leidy, in 1852, named the genus *Titanotherium* (=*Menodus*) from a similar fragment of a jaw found about 1846 in the Badlands of White River, South Dakota. The first titanothere jaw was discovered in South Dakota in 1846; its Asiatic relative was discovered in the heart of the Gobi Desert 76 years later, in 1922.

The first titanothere jaw (*Protitanotherium mongoliense*, figs. 784, 789, 792) to reach the American Museum, in the autumn of the year 1922, was found in the Shara Murun formation, which is more recent than the Irdin Manha. It was immediately recognized by the present writer as belonging to the genus *Protitanotherium* and as directly intermediate in size between *Protitanotherium emarginatum* and *Protitanotherium superbum*, both of the upper Eocene Uinta formation of Utah (level C of Uinta Basin). This determination was published October 17, 1923, and the description of the animal under the name *Protitanotherium mongoliense* was amply confirmed by discoveries made during the season of 1923.

Explorations in the Irdin Manha, Shara Murun, and still more recent Ardyn Obo formations continued for two seasons (1922, 1923) and yielded altogether remains of between 50 and 60 individual titanotheres, among which are many exceptionally fine skulls and jaws, numbering 45 in all, as listed below, and several limbs. After very careful shipment from the distant desert and skillful laboratory work, done chiefly by Messrs. George Olsen, Charles Lang, and Otto Falkenbach, the collection was assembled for critical examination, measurement, and comparison with the American titanotheres of northern Utah, of Wyoming, and of South Dakota, with most interesting results.

In Mongolia seven genera of American titanotheres are represented. *Dolichorhinus*, *Telmatherium*, *Protitanotherium*, *Menodus*, and *Brontops* are certainly identified; *Manteoceras* and *Metarhinus* are doubtfully

identified. The 10 species of these 7 genera are geologically distributed in ascending order in the Irdin Manha (upper Eocene), Shara Murun (summit of Eocene), and Ardyn Obo (lower Oligocene) formations, as shown in the accompanying table (p. 907). The discovery in Mongolia of 10 species belonging to these 7 genera of titanotheres confirms the generic conceptions and definitions of the American paleontologists Marsh, Hatcher, Wortman, and Osborn.

The seven generic names assigned to these species accord with those already established for the American specimens, namely:

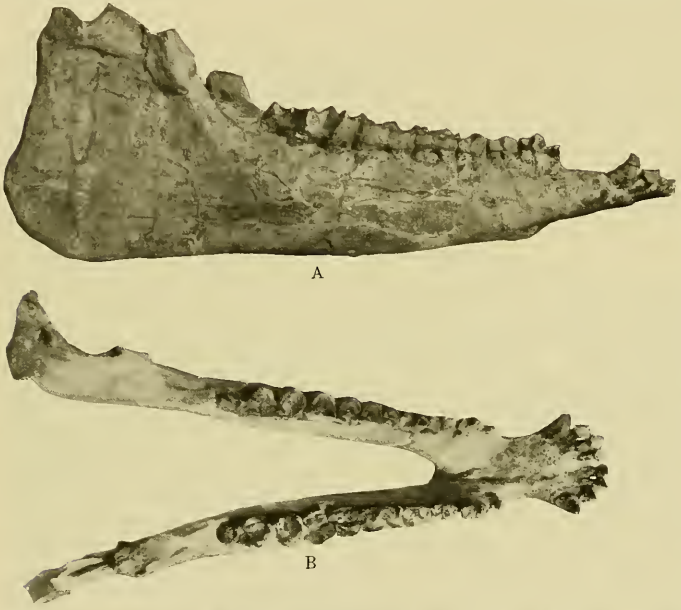


FIGURE 773.—Type lower jaw of *Protitanotherium grangeri* (Am. Mus. 20103) from the upper Eocene Irdin Manha formation of Mongolia

Probably a female specimen. Found at the locality indicated by a + in Figure 771. A, Side view; B, superior view. One-sixth natural size.

Metarhinus?, the diminutive amphibious Utah and Wyoming titanothere of Osborn.

Manteoceras?, the "prophet-horned" titanothere of Hatcher-Wortman.

Protitanotherium, the ancestor of the *Titanotherium* of Hatcher.

Telmatherium, the "swamp" titanothere of Marsh.

Dolichorhinus, the "long-nosed" titanothere of Hatcher.

Brontops, the "thunder-eyed" titanothere of Marsh.

Menodus, the "long-headed" titanothere of Pomel.

Most of the names assigned to species of these genera either refer to the region in which these remarkable specimens were found or are given in honor of the men who were instrumental in discovering them, namely:

Protitanotherium mongoliense, the titanothere first named from Mongolia.

Brontops gobiensis, the lower Oligocene "thunder-eyed" titanothere of the Gobi Desert.

Menodus mongoliensis, the first *Menodus* found in Mongolia.

Protitanotherium andrewsi, named in honor of Roy Chapman Andrews, leader of the third Asiatic expedition.

Protitanotherium grangeri, the first titanothere found in Mongolia, named in honor of Walter Granger, chief paleontologist of the expedition.

Telmatherium berkeyi, named in honor of Charles P. Berkey, chief geologist of the expedition, who picked up the first titanothere jaw.

Dolichorhinus kaiseni, named in honor of Peter Kaisen, who explored the Kaisen quarries of Ula Usu, Shara Murun formation.

Dolichorhinus olseni, named in honor of George Olsen, who discovered many fine titanotheres and was chief preparator of the titanothere collection.

Manteoceras? irdinensis, named in reference to its discovery in the Irdin Manha formation.

Metarhinus? mongoliensis, named in reference to its discovery in Mongolia.

The Ardyn Obo formation appears to represent the lower Oligocene, because the species *Brontops gobiensis* is very similar to certain species of Brontopinae, such as *Brontops brachycephalus* and *Teleodus avus*, found in the base of the Chadron formation, *Titanotherium* zone, South Dakota.

In the probably younger Oligocene formations of Mongolia known as the Houldjin and Hsanda Gol no remains of titanotheres have been discovered; the giant hornless rhinoceroses known as *Baluchitherium grangeri* are there the predominant mammals.

It therefore appears probable that the Brontotheriidae became extinct in Mongolia in the beginning of lower Oligocene time, whereas in western North America that family flourished and attained its zenith at the end of lower Oligocene time, when it suddenly became extinct.

These discoveries are historically so interesting that it appears desirable to give a complete list of the specimens of Mongolian titanotheres, some of which will in time be exhibited in the United States National Museum and other great museums of this and other countries. In this list the numbers are those assigned to the specimens in the American Museum of Natural History.

Locality, identification, and character of remains of 26 specimens of skulls, jaws, and other parts of skeletons of titanotheres collected from the Irdin Manha formation (upper Eocene) at places near the Kalgan-Urga telegraph line, in southeastern Gobi, Mongolia

[After field catalog and notes of Walter Granger]

Species	Mus. No.	Character of remains
Two miles north of telegraph line		
Manteoceras? irdinensis Osborn, type	20111	A right lower jaw.
(Specimen misplaced)	20117	Field label, "titanothere lower jaw."
Protitanotherium grangeri, referred	20120	A perfect portion of right maxilla.
Do	20122	A juvenile palate and grinding teeth.
Do	20123	Fragment of left maxilla and grinding teeth.
Do	20126	Fragment of left ramus with grinding teeth.
Telmatherium berkeyi, paratype	20121	A perfect left maxilla with grinding teeth.
One mile north of telegraph line		
Protitanotherium grangeri, referred	20105	A large adult male jaw with teeth.
One-half mile north of telegraph line		
Protitanotherium grangeri, referred	20108	A small female right maxilla and grinding teeth.
Dolichorhinus olseni Osborn, type	20109	A fine pair of jaws.
Telmatherium berkeyi, referred	20125	Left maxilla with premolar teeth.
Do	20124	Right jaw with well-preserved grinders.
One-half mile south of telegraph line		
Protitanotherium grangeri Osborn, type	20103	Female skull and jaws well preserved; incisors, canines, fragmentary molars.
Protitanotherium grangeri, referred	19179	Left jaw and symphysis, with 6 grinders. *The first titanothere found in Mongolia.*
Do	20113	Facial portion of female cranium, with anterior grinders.
Do	20114	Anterior portion of female cranium, with dentition.
Do	20119	Fragment left jaw with 4 grinding teeth.
One mile south of telegraph line		
Protitanotherium grangeri, referred	20112	Young male right ramus of jaw, with 6 grinding teeth.
Protitanotherium grangeri?, referred	20110	Large male jaws, with complete dentition.
Telmatherium berkeyi Osborn, type	20106	Adult female lower jaws; right maxilla, canines, and grinders.
Telmatherium berkeyi, paratype	20107	Anterior half of jaw; canine and inferior grinders.
Telmatherium berkeyi, referred	20127	Palate and superior grinders.
Do	20115	Juvenile lower jaw, with incisors and grinder.
One-half mile west of telegraph line		
Protitanotherium grangeri, referred	20104	Very large male jaw with nearly complete dentition.
Exact locality unrecorded		
Metarhinus? mongoliensis Osborn, type	20167	Small lower jaw, 2 grinding teeth, milk superior grinders.
Protitanotherium grangeri, referred	20171	Right humerus, 2 right ulnae, left ulna and radius, axis, right tibia.

Locality, identification, and character of remains of 27 skulls, jaws, and other parts of skeletons of titanotheres collected from the Shara Murun formation (uppermost Eocene) near the locality Ula Usu, on the Kalgan-Uliassutai trail, in southeastern Gobi, Mongolia

[After field catalog and notes of Walter Granger]

Species	Mus. No.	Character of remains
Dolichorhinus kaiseni Osborn, type	20252	Male skull and jaws; nearly complete dentition.
Dolichorhinus kaiseni, paratype	20257	Palate and basicranium; complete dentition.
Dolichorhinus kaiseni, referred	20255	Female skull and jaws; nearly complete dentition.
Do	20260	Male skull and jaws; complete dentition.
Protitanotherium mongoliense Osborn, type	18653	Right ramus, fragment, with 6 grinding teeth. First titanothere to reach American Museum from Mongolia.
Protitanotherium mongoliense, neotype	20263	Palate and dentition nearly complete.
Protitanotherium mongoliense, referred	20256	Palate, canine, superior grinders, lower jaws.
Do	20261	Female skull complete but crushed; incisors, canine, grinders.
Do	20270	Right maxilla and zygoma; superior grinders.
Do	20273	Fine pair of jaws, lacking symphysis; inferior grinders.
Protitanotherium andrewsi Osborn, type	20271	Complete male skull and dentition; nasals wanting.
Protitanotherium andrewsi, paratype	20251	Male? Left ramus; inferior grinders.
Protitanotherium andrewsi, referred	20254	Male skull; superior dentition.
Do	20262	Jaws; symphysis, upper incisors, and grinders.
Do	20269	Symphysis of jaws with canines.
Do	20280	Juvenile palate, deciduous premolars, first and second molars.
Do	20272	Fine jaw, male; inferior dentition.
Not determined (pro-Menodus mongoliensis phylum?).	20253	Premaxilla, incisor; ulna, femur, several vertebrae and foot bones.
Not determined	20265	Maxilla fragment.
Do	20268	Left ramus of lower jaws.
Not determined (Protitanotherium?)	20258	Fore foot, with distal end of ulna and radius.
Protitanotherium andrewsi?, referred	20259	Part of fore foot (metapodials).
Not determined (Protitanotherium)	20267	Associated foot bones.
Protitantherium mongoliense, referred	20274	Incomplete hind foot.
Not determined (Protitanotherium?)	20275	Fore and hind foot bones.
	20276	
Protitanotherium mongoliense, referred	20277	Complete hind limb and foot.
Protitantotherium andrewsi, referred	20327	Right humerus, 2 right tibiae, left tibia, miscellaneous foot bones.

Locality, identification, and character of teeth, jaws, and skull collected from the Ardyn Obo formation (lower Oligocene) on the Kalgan-Uliassutai trail, southeastern Gobi, Mongolia

[After field catalog and notes of Walter Granger]

Species	Mus. No.	Character of remains
Brontops gobiensis Osborn, type	20354	Crushed skull, collected July 2, 1923.
Brontops gobiensis, referred	20353	Symphyseal region of lower jaw, collected June 30, 1923.
Menodus mongoliensis Osborn, type	20351	Part of lower grinding tooth, collected June 29, 1923.

GENERIC AND SPECIFIC CHARACTERS OF THE MONGOLIAN TITANOTHERES

Next to the discovery of titanotheres in Mongolia the most gratifying feature of the results of the exploration is that all the species thus far found belong to genera similar to those previously discovered in the Rocky Mountain region of North America. This generic affinity enables us to establish four or perhaps five lines of titanothere migration between central Asia and North America. These genera, named in ascending or progressive order of evolution, are as follows:

Lower Oligocene *Brontops* of the Ardyn Obo formation; extremely broad-headed, similar to the *Brontops* of South Dakota.

Lower Oligocene *Menodus* of the Ardyn Obo formation; long-headed, somewhat similar to the *Menodus giganteus* of South Dakota.

Upper Eocene *Protitanotherium* of the Irdin Manha and Shara Murun formations; a large animal, similar to the *Protitanotherium* of the Uinta formation of Utah.

Telmatherium of the Irdin Manha formation; long-headed, deep-jawed, similar to the *Telmatherium* of the Bridger and Uinta formations of Wyoming and Utah.

Dolichorhinus of the Irdin Manha and Shara Murun formations; the "long-nosed" titanothere, similar to the *Dolichorhinus*

of the upper part of the Bridger formation of Wyoming and Utah.

Manteoceras (generic reference doubtful) of the Irdin Manha formation; the "prophet-horned" titanothere, somewhat similar to the *Manteoceras* of the upper part of the Bridger formation of Wyoming and the Uinta Basin of Utah.

Metarhinus (generic reference doubtful) of the Irdin Manha formation; somewhat similar in its diminutive size to the *Metarhinus fluviatilis* of northern Utah and southern Wyoming.

The distinctive characters of four well-established American genera—*Dolichorhinus, Telmatherium, Protitanotherium,* and *Brontops*—may be contrasted with those shown in the following table, which is based upon the chief characters of the Asiatic forms:

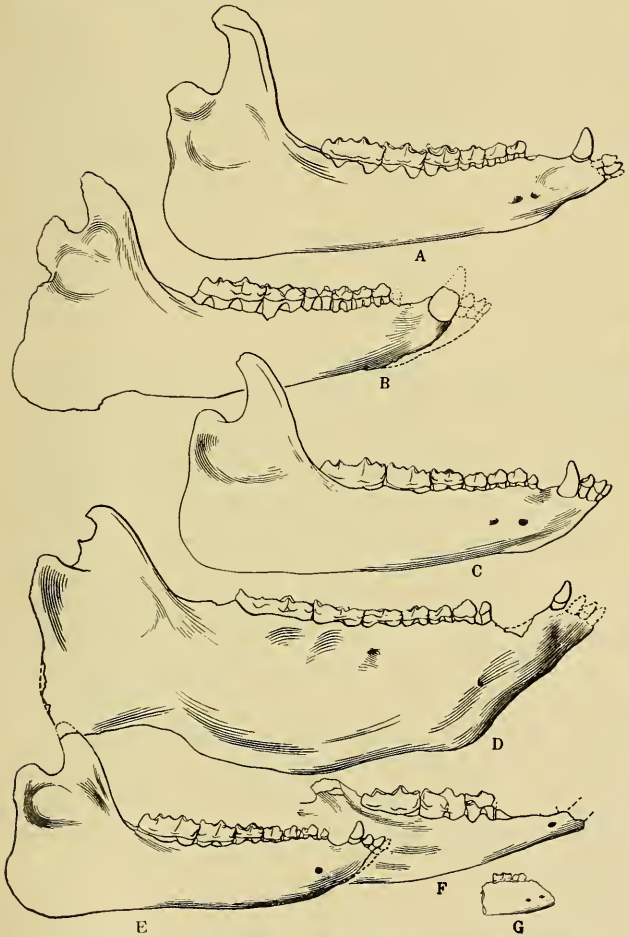


FIGURE 774.—Comparative views of jaws of upper Eocene titanotheres from the Irdin Manha and Shara Murun formations of Mongolia

A, *Protitanotherium andrewsi*, large male jaw (Am. Mus. 20272), Shara Murun formation (compare fig. 786); B, *Protitanotherium grangeri*, large male jaw (Am. Mus. 20105), Irdin Manha formation; C. *Protitanotherium grangeri*, large male jaw (Am. Mus. 20104), Irdin Manha formation; D, *Telmatherium berkeyi*, type female jaw (Am. Mus. 20106), Irdin Manha formation; E, *Dolichorhinus olseni*, type male jaw (Am. Mus. 20109), Irdin Manha formation; F, *Manteoceros? irdinensis*, type jaw (Am. Mus. 20111), Irdin Manha formation; G, *Metarhinus? mongoliensis*, type jaw (Am. Mus. 20167), Irdin Manha formation. All one-eighth natural size.

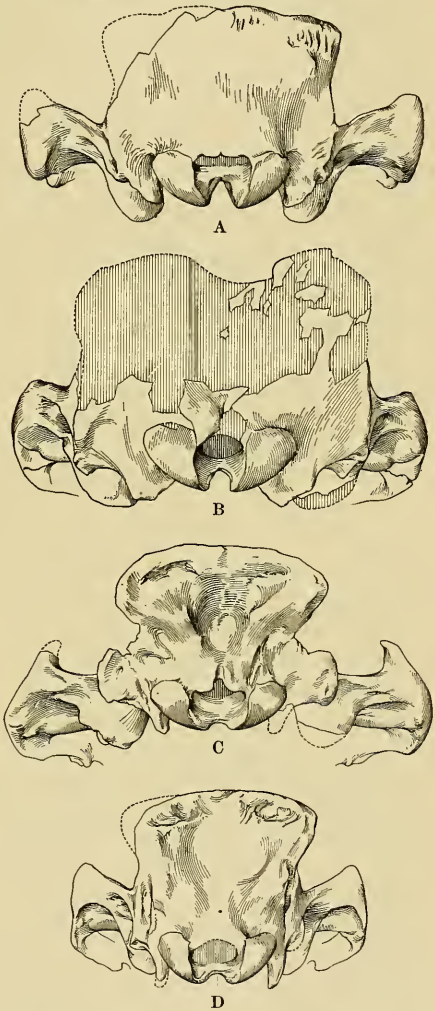


FIGURE 775.—Comparative occipital views of the chief titanotheres of Mongolia in descending geologic order

A, *Brontops gobiensis*, occiput of type cranium (Am. Mus. 20354), Ardyn Obo formation; B, *Protitanotherium andrewsi*, occiput of type cranium (Am. Mus. 20271), Shara Murun formation; C, *Protitanotherium grangeri*, occiput of type cranium (Am. Mus. 20103), Irdin Manha formation; D, *Dolichorhinus koiseni*, occiput of type cranium (Am. Mus. 20252), Shara Murun formation. All one-sixth natural size.

Distinctive characters of four genera of titanotheres

	Dolichorhinus olseni, D. kaiseni	Telmatherium berkeyi	Protitanotherium grangeri, P. mongoliense, P. andrewsi	Brontops gobiensis
Cranial proportions	Of small size; long, narrow, shallow jaws.	Of large size; deep, elongate maxillae and jaws.	Of large and increasing size; broad zygomata.	Of small size; extremely broad headed.
Cranio-zygomatic index.	Approximately 47	Unknown	Approximately 69–58	Approximately 74.
Zygomata	Slender, flattened, angulate.	Unknown	Strong, broadly expanding.	Very strong, broadly arched.
Jaws	Elongate, slender, angulate, angle retroverted; chin symphysis shallow.	Very deep, bathygnathous; chin symphysis deep.	Jaws of medium depth; chin symphysis shallow.	Chin symphysis robust, convex.
Nasals	Long, narrow, strongly decurved at sides.	Unknown	Broad, long, shallow	Broad, obtuse.
Horns	Rounded, short, obtuse	Unknown, probably rudimentary.	Elongate anteroposteriorly	Rounded anteroposteriorly.
Cranial vertex	Narrow, cylindrical, convex.	Unknown	Broadening to saddle shape.	Saddle-shaped.
Occiput	Relatively small, narrow	Unknown	Of increasing breadth and height.	Broad.
Incisors	Of medium size, spatulate, postcingulate; second lower incisors slightly enlarged.	Of great size, convexo-concave; second lower incisors enlarged.	Medium, tending to rounded summits; third incisors enlarged.	Blunt or rounded summits.
Canines	Short, rounded, incurved	Very large, pointed, strongly incurved.	Large, rounded, biconvex, recurved.	Rounded, obtuse.
Premolars	Deuterocones large, tetartocones rudimentary.	Deuterocones greatly enlarged, tetartocones rudimentary.	Deuterocones broad, tetartocones increasing in size.	Prominent rounded tetartocones.
Molars	Inferior molars narrow, hypocones absent in m^3.	Extremely narrow, hypocones prominent in m^3.	Broader, hypocones absent or rudimentary in m^3.	Extremely broad, hypocones rudimentary or absent in m^3.

NOTE.—The single lower molar of a species of *Menodus*, discovered in the *Brontops gobiensis* zone, represents a much larger animal—long-headed, narrow-toothed—to which the name *Menodus mongoliensis* has been assigned.

DESCRIPTIONS OF SPECIES

SUBFAMILY DOLICHORHININAE

Dolichorhinus Hatcher, 1895

The generic characters of this long-nosed titanothere as it lived in Mongolia are readily determined by comparing the single type jaw of *Dolichorhinus olseni*, from the Irdin Manha formation, with the three exceptionally well-preserved skulls and jaws of *Dolichorhinus kaiseni*, including also palate and basicranium with complete dentition, from the overlying Shara Murun formation. The genus is named from its long, narrow, transversely arched nasals, which descend in sharp, broad plates at the sides. No other titanothere exhibits this feature. The cranial proportions are correspondingly elongate, laterally compressed, arched superiorly with slender, flattened zygomatic arches correlated with relatively feeble powers of mastication; the breadth-length index, 47 (length 695 mm., breadth 330 mm.), contrasts with an index of 69 in a skull of *Protitanotherium grangeri* of the same basilar length, namely, 695 millimeters. The horns are not elongate but are rounded, short, obtuse, and much more prominent than in any known American species. The jaws are elongate, slender, angulate, with slender coronoid processes. The dentition harmonizes with the relatively feeble masticating and offensive powers, the canines being relatively small, the incisors of medium size with posterior cingula, the second lower incisors slightly enlarged. In these, as in the American species, the premolars are simple and have large median internal deuterocones and rudimentary tetartocones.

In the Irdin Manha formation occurs the more primitive species *Dolichorhinus olseni*, represented by a beautifully preserved type jaw, and in the Shara Murun formation occurs the more progressive species *Dolichorhinus kaiseni*, represented by three skulls and jaws and one complete palate and basicranium, as enumerated in the tables given above.

Measurements of lower jaw and teeth of two species of Dolichorhinus, in millimeters

	D. olseni, type jaw (Am. Mus. 20109)		D. kaiseni, referred jaw (Am. Mus. 20260) and type jaw (Am. Mus. 20252)	
	Right ramus	Left ramus	Right ramus	Left ramus
P_2–m_3	258	256	276	277
M_1–m_3	182	175	190	190
M^1–m^3	(?)	(?)	164	162
P_4, ap. by tr	28×20	28×20	31×22	29×26
P_4, index	71	71	71	90
M_3, ap. by tr	88×32	86×35	85×39	[a] 83×40
M_3, index	36	41	46	48
Basilar length of skull, condyles to premaxillae			660–695	
Total length of jaw, condyles to incisive border	536–538		555–580	
P^2–m^3			230–262	
P_2–m_3	256–258		265–277	

[a] Estimated.

Dolichorhinus olseni Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type locality and geologic level.—Half a mile north of the Kalgan-Urga telegraph line, southeastern Gobi, Mongolia; Irdin Manha formation (upper Eocene).

Materials.—This species is based upon a fine pair of jaws, the type of *Dolichorhinus olseni* Osborn (Am. Mus. 20109, fig. 774, E), found half a mile north of the Kalgan-Urga telegraph line. Species of this genus appear to be relatively rare in the Irdin Manha, whereas the more progressive species *Dolichorhinus kaiseni* is quite abundant in the overlying Shara Murun formation.

Specific characters.—The measurements given above show that the type jaw of *Dolichorhinus olseni* is throughout inferior in size to the referred jaw (Am. Mus. 20260) and to the type jaw (Am. Mus. 20252) of *Dolichorhinus kaiseni*, as shown by the type figure of *D. olseni* (fig. 774) and more clearly in a comparison of the type specimen of *D. olseni* itself with the three jaws of *D. kaiseni* (Am. Mus. 20257, 20255, and 20260).

We observe the following less progressive characters: (1) Canines narrow and sharply pointed; (2) lateral first and second incisors more pointed, less broadly cupped or cingulate posteriorly; (3) first premolars small, single-fanged, pointed; second and third premolars, p_{2-3}, lacking cup-shaped concavity of talonid which is present only in p_4—that is, all rudiments of entoconid and all evidence of broadening of talonid are lacking in *D. olseni* in p_{2-3}; these teeth are far more primitive than the corresponding teeth of *D. kaiseni*; (4) the fourth inferior premolar still very primitive, exhibiting a shallow concavity of the trigonid, a relatively broad, slightly concave talonid.

Dolichorhinus kaiseni Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type locality and geologic level.—Near Ula Usu on the Kalgan-Uliassutai trail, southeastern Gobi, Mongolia; Shara Murun formation (uppermost Eocene).

Materials.—This species is based upon the type (Am. Mus. 20252), a male skull and jaws, nearly complete dentition, and the paratype (Am. Mus. 20257), a palate and basicranium, complete dentition. There are also two referred specimens, namely, Am. Mus. 20255, a female skull and jaws, nearly complete dentition, and Am. Mus. 20260, a male skull and jaws, complete dentition. Because of the tubular air spaces filling the arched cranium, the three crania were severely crushed, and the broken parts, assembled through most careful field collecting, were pieced together with great skill by Mr. George Olsen. The cream-white external appearance of the skull is quite different from the rust-brown color of the Irdin Manha specimens.

Specific characters.—As shown in the comparative series of measurements above, *Dolichorhinus kaiseni* is superior in length of jaw and in all its dental measurements to *Dolichorhinus olseni;* the breadth-length indices of the fourth inferior premolar, p_4, and of the third inferior molar, m_3, are approximately the same in the two species. These relatively long, narrow indices are harmonic with the extremely dolichocephalic, elongate cranium and jaws. As in several of the Wyoming and Utah species of this genus, the small canines, even in the males, are in compensation for the precociously developed horn swellings; these bony horns are relatively much more prominent than in *Dolichorhinus hyognathus* (= *cornutus*) of the uppermost part of the Bridger formation of the Washakie Basin, Wyoming, and the Uinta Basin, Utah.

The type cranium (Am. Mus. 20252), the paratype cranium (Am. Mus. 20257), the fine referred cranium (Am. Mus. 20260), and the more mature referred cranium (Am. Mus. 20255) are singularly uniform in their characters and apparently represent different stages of growth rather than different phases of evolutionary progress. Although the canines are relatively small as compared with the robust canines of *Protitanotherium,* we judge that these four crania belong to male individuals because of the uniform size of the canines and of the uniform development of the tuberous bony horns. These horns project outward rather than upward; the fore-and-aft diameter of the horn base is short as compared with the elongate horns of *Protitanotherium.* Below them are the flaring sides of the

premaxillo-nasal junction, which are extended forward into the hooded nasals that resemble the inverted, rounded prow of a boat. This exaggerated evolution of the long and narrow nasals suggested the name *Dolichorhinus cornutus* for the "horned long-nosed" titanothere of Wyoming and Utah. Back of this extension is the long, tubular cranium, which in section is quite hollow, including the large tubular air chambers which completely conceal the small brain case below.

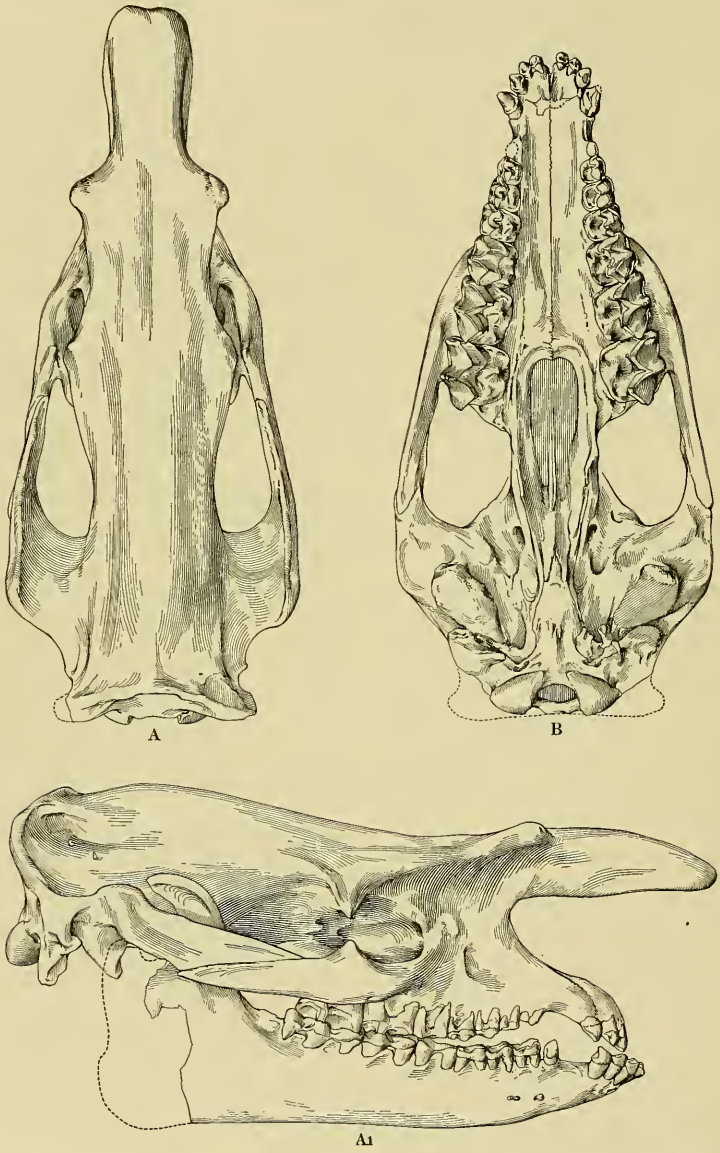


FIGURE 776.—Crania and jaws of the type and paratype of *Dolichorhinus kaiseni*, from the Shara Murun formation

A, Superior view of type cranium (Am. Mus. 20252); A1, right lateral view of type cranium and jaws (Am. Mus. 20252); B, palatal view of paratype cranium (Am. Mus. 20257). All one-sixth natural size.

As shown in our cranial sections of *Dolichorhinus hyognathus* (=*cornutus*) of Wyoming and Utah, the occiput is relatively small, low, flaring toward the top; the condyles are relatively small, sharply convex; the zygomata are extremely slender, elongate, sharply angulate as they turn inward toward the postglenoid processes; anteriorly there is a rounded rather than angulate suborbital malar bar. The mandibular rami are readily distinguished from those of *Protitanotherium* by three characters—(1) the marked external muscular sculpturing of the coronoid and condylar regions; (2) the backward extension and downward curvature of

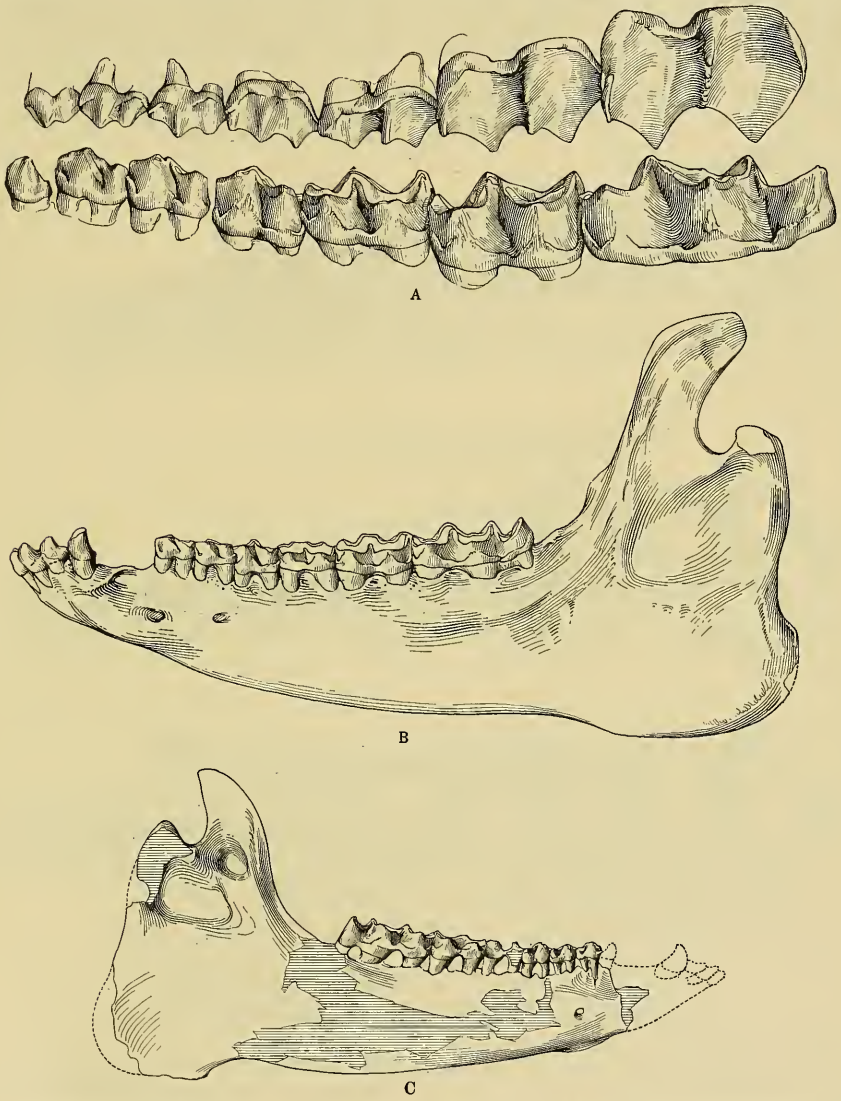


FIGURE 777.—Comparative views of the superior and inferior grinding teeth of *Dolichorhinus kaiseni* and of the lower jaws of *D. kaiseni* and *Protitanotherium grangeri*

A, External aspect of the grinding teeth of *D. kaiseni* (Am. Mus. 20260), one-half natural size; B, left lateral aspect of female jaw of *D. kaiseni* (Am. Mus. 20255), one-fourth natural size; C, right lateral aspect of *Protitanotherium grangeri* jaw (Am. Mus. 20105), one-sixth natural size. Observe the marked difference in the form of the coronoid, in the elevation of the condyle, and in the contour of the angle in the lower border of the ramus, in the two species.

the angle; (3) the relatively shallow rami which decrease in depth anteriorly, passing into the laterally constricted diastema borders which expand again into the broadened borders for the cutting teeth, a character similar to that which gave the specific name *hyognathus* (suilline-jawed) to the type from the

Dental characters.—The dentition of *D. kaiseni*, as distinguished from the more ancient, primitive, and slender *Dolichorhinus olseni* of the Irdin Manha, is displayed in the aged type (Am. Mus. 20252), in the fully adult referred skull and jaws (Am. Mus. 20255), in the somewhat less adult referred skull and jaws (Am.

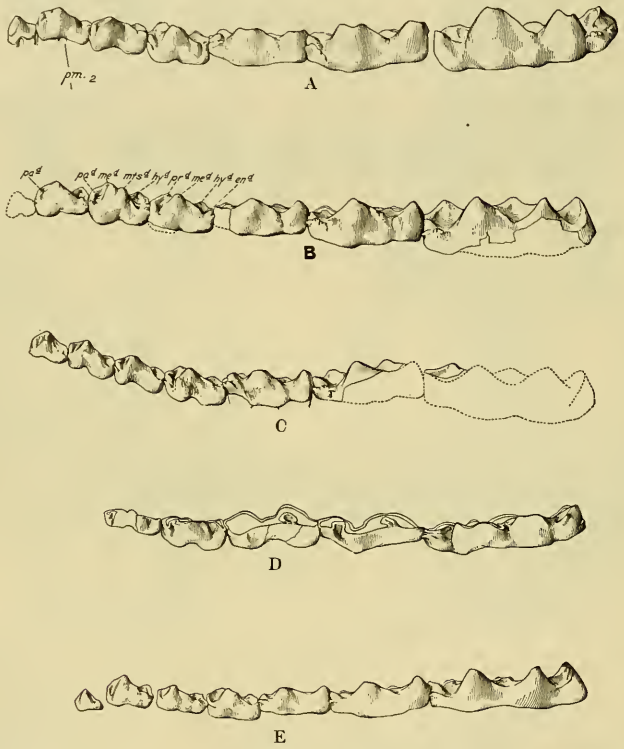


FIGURE 778.—Internal aspect of the inferior grinding teeth of five species of titanotheres from upper Eocene beds of Mongolia, Burma, and Utah, in descending order

A, *Protitanotherium superbum*, Am. Mus. 2501 (type), Uinta formation, Utah (horizon C of Uinta Basin); B, *Protitanotherium mongoliense*, Am. Mus. 18653 (type), Shara Murun formation, Mongolia; C, *Protitanotherium emorginotum*, Princeton Mus. 11242 (type), Uinta formation, Utah; D, titanothere of an undetermined species (Am. Mus. 20014), Pondaung formation, Burma; E, *Protitanotherium grangeri*, Am. Mus. 20103 (type), Irdin Manha formation, Mongolia. Observe especially the progressive evolution of the talonid and the ascending rectigradations in the premolar teeth, p_{2-4}, of *Protitanotherium*. *Protitanotherium mongoliense* of the Shara Murun formation shows a marked advance upon *P. grangeri* of the Irdin Manha in the development of the entoconid; *P. superbum* of the Uinta C is somewhat more progressive than *P. mongoliense* of the Shara Murun. All figures one-third natural size.

Washakie Basin of Wyoming, as named by Scott and Osborn.

It is this intermingling of the characters observed in the American specimens with those discovered in this Mongolian species of *Dolichorhinus* that gives these imals such exceptional interest. Other details of character in the four aspects of the cranium, lateral, superior, palatal, and occipital, are well portrayed in the accompanying figures.

Mus. 20260), and in the paratype (Am. Mus. 20257) of similar age and is singularly uniform in its progressive evolution.

The incisors diminish in size from $I\frac{3}{3}$ to $I\frac{1}{1}$, from the lateral to the median. All the inferior incisors exhibit broad, postcingulate, almost cup-shaped bases, summits constricting rapidly, crowns diminishing in height from $I\frac{3}{3}$ to $I\frac{1}{1}$. A pair of lower incisors (i_1, i_2) display this cup-shaped, postcingulate character,

whereas the corresponding pair of upper incisors (i^1, i^2) display blunted summits or apices characteristic of *Protitanotherium*, although the rounding and convexity of the crown are not carried so far, there being a distinct trace of a postcingulum; this character is a convergent one with *Protitanotherium* and the Oligocene titanotheres generally.

The superior premolars are relatively elongate and laterally compressed. Each possesses a prominent, elongated deuterocone, which extends backward into a low, subsiding crest on which a faint swelling indicates the rudiment of a tetartocone. This rudiment diminishes in prominence as we pass from p^2 to p^4, in which there is no trace of the tetartocone swelling. Thus, as in *Protitanotherium*, the first, second, and third superior premolars acquire the tetartocone more rapidly than the fourth premolar.

The molars are also relatively elongate and narrow, as compared with those of *Protitanotherium*. Thus the ectolophs are relatively elongated; the parastyle, mesostyle, and hypostyle are very sharp and prominent, as compared with those in the contemporary *Protitanotherium monogoliense*; the inner half of the crown supports low protocones and hypocones, except in m^3, in which there is only an extremely sessile prominence of the enamel representing the hypocone region, and the cingulum extends broadly around the posterior end of the crown. The superior and inferior premolars are harmonic in the retarded development of the secondary cones, styles, and stylids. The entoconid below is represented by a ridge continuous with the rudimentary metastylid. No distinct entoconid appears below, in keeping with the absence of a distinct tetartocone above.

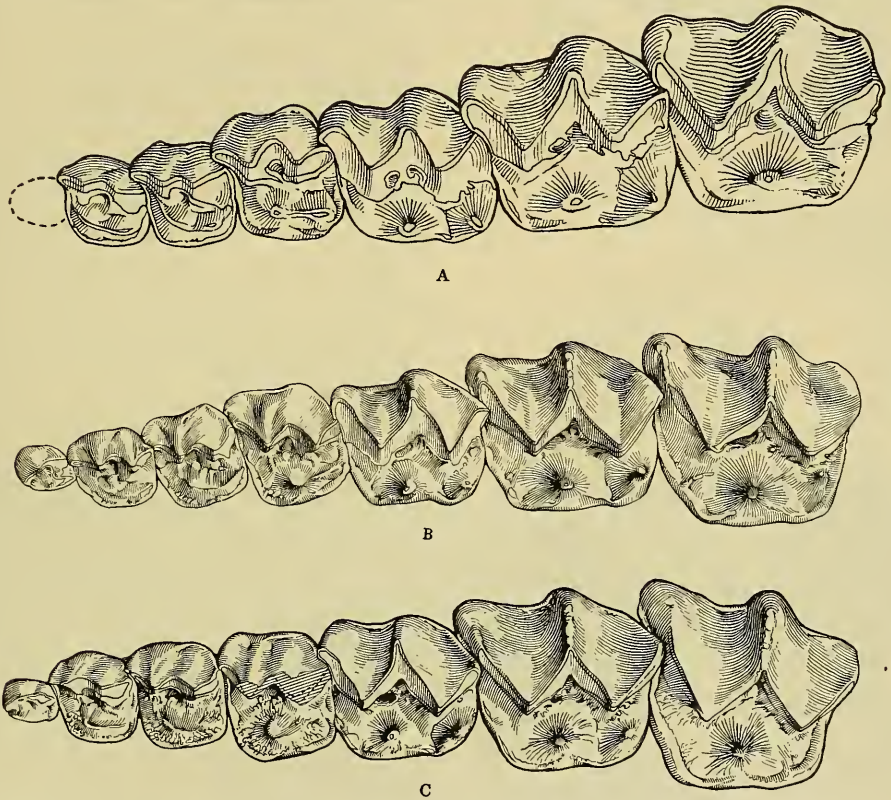


FIGURE 779.—Comparison of the superior grinding teeth of *Protitanotherium andrewsi* and of *Protitanotherium mongoliense* to show the progressive development of the tetartocones in the superior premolars and of the hypocones in the third superior molars

A, Type of *Protitanotherium andrewsi* (Am. Mus. 20271); B, referred *Protitanotherium andrewsi* (Am. Mus. 20254); C, neotype of *Protitanotherium mongoliense* (Am. Mus. 20263). About one-half natural size. Observe especially the progressive development of the tetartocones in p^{2-4}; also of the rudimentary hypocone in m^3.

Measurements of type, paratype, and two referred specimens of Dolichorhinus kaiseni, in millimeters

	Type (Am. Mus. 20252)	Referred specimens		Paratype (Am. Mus. 20257)
		Am. Mus. 20260	Am. Mus. 20255	
Anteroposterior basilar length of skull	660	685	655	695
Transverse zygomatic width of skull	----	----	----	330
Breadth-length cranial index	----	----	----	47
P^2–m^3:				
Right	----	250	----	262
Left	230	245	236	257
Breadth-length index, m^3:				
Right	----	98	100	105
Left	98	102	100	91
P_2–m_3:				
Right	268	276	----	----
Left	271	277	265	----
M_1–m_3:				
Right	[a] 182	190	----	----
Left	182	190	180	----
M_3, ap. by tr.:				
Right	85×39	86×31	----	----
Left	[a]83×40	92×33	86×31	----
M_3, index:				
Right	46	36	----	----
Left	48	36	36	----

[a] Estimated.

SUBFAMILY MANTEOCERATINAE (BRONTOPINAE)

Protitanotherium Hatcher, 1895

Generic characters.—The generic characters of this broad-nosed titanothere as it lived in Mongolia are readily inferred by comparing it with the numerous skulls and jaws of the primitive species *Protitanotherium grangeri*, from the Irdin Manha formation, and of the more progressive species *Protitanotherium mongoliense* and *Protitanotherium andrewsi*, from the overlying Shara Murun formation. The genus takes its name from the resemblance of its long, broad, shallow, and gently decurved nasal bones to those of *Menodus* (= *Titanotherium*) and of *Brontops* in South Dakota. The low, elongate, transversely narrow bony horns resemble those of *Brontops brachycephalus*. The cranial proportions are correspondingly broad, depressed; the stout, broadly expanding zygomatic arches are correlated with relatively strong powers of mastication; the breadth-length index of 69 (*P. grangeri*; length 695 mm., breadth 480 mm., estimated) contrasts with an index of 47 in a skull of *Dolichorhinus kaiseni* of the same basilar length, 695 millimeters. The nasofrontal bony horns also are elongate and are low, oblong, obtuse, but less obtusely prominent than in *Dolichorhinus*. The jaws are robust and have prominent coronoid processes and shallow symphysis as compared with *Brontops gobiensis*. The dentition harmonizes with the strong masticating power of

FIGURE 780.—Jaws of *Protitanotherium grangeri* in place, Irdin Manha formation, upper Eocene of Mongolia
Messrs. Osborn, Granger, and the Chinese assistant Kan Chan Pou in the fore-ground. After Am. Mus. negative No. 251583, by R. C. Andrews.

the grinders and the offensive power of the canines, which are relatively large, especially in the robust males. The incisors are of medium size with obtuse cingula, diminishing in size from the lateral to the median, the summits tending to become rounded and obtuse in *P. andrewsi*. As in the American species, the superior and inferior premolars become progressively molariform.

Comparative measurements of three species of Protitanotherium, in millimeters

	P. grangeri, Am. Mus. 20103 (type)	P. mongoliense, Am. Mus. 18653 (type), 20263 (neotype), 20261 (referred)	P. andrewsi. Am. Mus. 20271 (type), 20251 (paratype)
Basilar length of skull (anteroposterior)	695	677 (20261)	757 (20271)
Transverse measurement of skull across zygomata	[a] 480		[a] 440 (20271)
Cranio-zygomatic index	69		[a] 58
P^2–m^3	242	269 (20263)	283 (20271)
M^3, ap. by tr	61×62	71×71 (20263)	72×71–75 (20271)
M^3, index	101	100 (20263)	99–103 (20271)
M_3, ap. by tr	85×34	88×36 (18653)	95×37 (20251)
M_3, index	40	41	39
P_2–m_3	174	289 (18653)	308 (20251)

[a] Estimated.

Protitanotherium grangeri Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type locality and geologic level.—Half a mile south of the Kalgan-Urga telegraph line, southeastern Gobi, Mongolia; Irdin Manha formation (upper Eocene, *Protitanotherium grangeri* zone).

Materials.—Our knowledge of this species is based on the materials found north and south of the Kalgan-Urga telegraph line, including the type (Am. Mus. 20103), female skull and jaws well preserved, incisors, canines, fragmentary molars, also four specimens (Am. Mus. 20120, 20122, 20123, 20126) found 2 miles north of the telegraph line, one specimen (Am. Mus. 20105) found 1 mile north of the telegraph line, another (Am. Mus. 20108) found half a mile north of the telegraph line, four (Am. Mus. 19179, 20113, 20114, 20119) found half a mile south of the telegraph line, two (Am. Mus. 20112, 20110) found 1 mile south of the telegraph line, and one (Am. Mus. 20104) found half a mile west of the telegraph line.

This very rich and abundant material is supplemented by remains of fore and hind limbs of both the right and left sides (Am. Mus. 20171) belonging to several individuals. Consequently, while we know the cranial and dental characters of *Protitanotherium grangeri* of both sexes perfectly, we have still much to learn regarding the skeleton.

Specific characters.—The exceptional features of the type cranium (Am. Mus. 20103), such as (*a*) the horseshoe-shaped concavity bordering the posterior

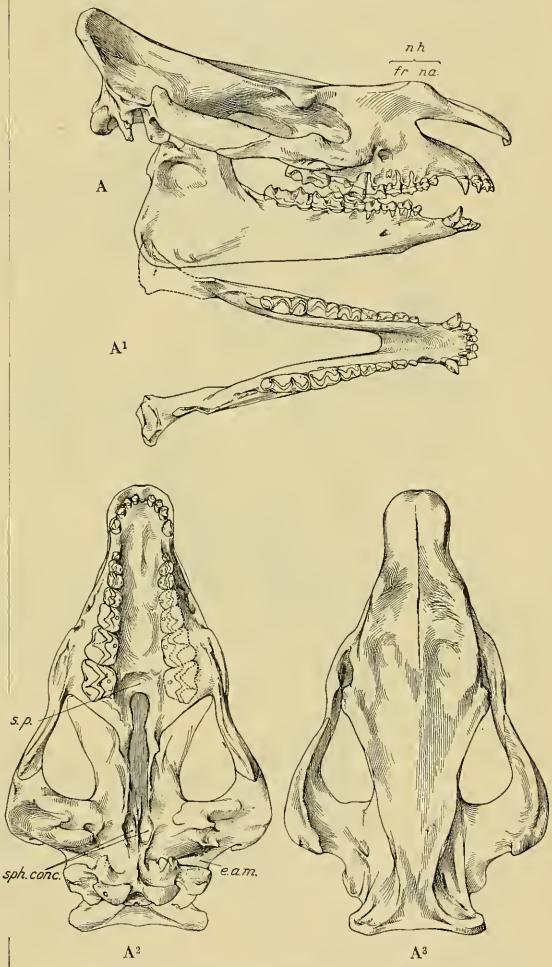


FIGURE 781.—*Protitanotherium grangeri*, Am. Mus. 20103 (type)

A well-preserved female skull and jaws, with incisors, canines, and fragmentary molars, altered by vertical crushing of the symphyseal region of the jaw. Discovered half a mile south of the Kalgan-Urga telegraph line. A, Lateral view, right side; A^1, lower jaw, superior view; A^2, skull, inferior view; A^3, skull, superior view. Original drawing. One-tenth natural size.

nares and (*b*) the deep pits on either side of the presphenoid, characters observed also in specimens of *Dolichorhinus* (*a*) and of *Sphenocoelus* (*b*), led us at first to regard this type as related to the above genera.

The real propinquity of the species *grangeri* to *Protitanotherium* is, however, firmly established by the

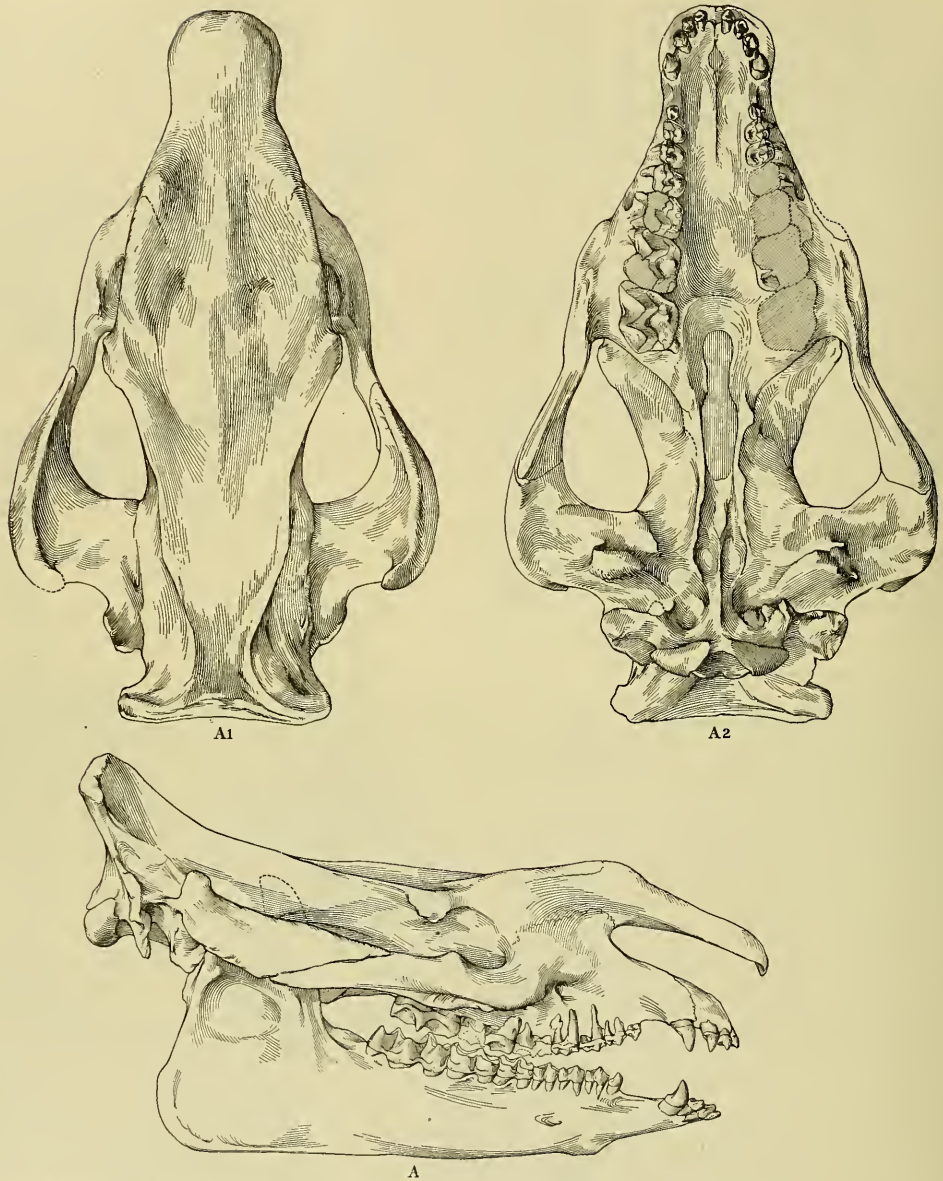


FIGURE 782.—Type female cranium and jaws of *Protitanotherium grangeri* Osborn (Am. Mus. 20103), Irdin Manha formation, half a mile south of the Kalgan-Urga telegraph line. Revised drawing

A, Right lateral view of skull and jaws; A_1, superior view of skull; A_2, palatal view of skull. All one-sixth natural size. Observe especially the concave depression surrounding the anterior border of the posterior nares; also the two concave sphenoidal pits in the basal axes of the cranium between the two postglenoid processes.

elongate horns, the broad, shovel-shaped nasals, the broad sweep of the zygomatic arches, and the saddle-shaped cranial top; also, in the dentition, by the sharply incurved canines, the enlarged lateral superior and inferior third incisors, and the diminishing second and first incisors, which in this species retain their pointed, postcingulate form.

Dentition.—The ancestral or primitive character of the grinding teeth of *P. grangeri*, as compared with the more progressive grinders of *Protitanotherium mongoliense* and of *P. andrewsi*, is seen in the absolutely simple internal deuterocones without even a rudiment of the tetartocones. The ancestral character is observed also in the absence of any trace of a hypocone in m^3 (compare type Am. Mus. 20103, also referred Am. Mus. 20114, 20108, and 20120). These non-progressive superior grinders indicate that *Protitanotherium grangeri* is geologically far more ancient than the *P. mongoliense* and the *P. andrewsi* of the Shara Murun. The inferior premolars are correspondingly simple (type Am. Mus. 20103, referred Am. Mus. 20112, 20126); there is barely a rudiment of the entoconid, or entoconid shelf, on the inner side of the narrow posterior lobe, whereas in *P. mongoliense* this lobe is broadened with a more or less prominent entoconid rudiment. (See figs. 777, 778, 779.)

Cranium.—The type of *P. grangeri* is a female skull with small, sharply recurved canines, whereas the males of *P. grangeri* (Am. Mus. 20112) have relatively prominent, lanceolate canines, suggesting those of the true *Menodus* (= *Titanotherium*), but the broadened sub-brachycephalic cranium and shallow jaws do not resemble those of the true *Menodus*.

Our conclusion is that the female type cranium of *Protitanotherium grangeri* exhibits the following distinctive characters: (1) Concave postpalatal border (2) basipresphenoidal pits, (3) subangulate characters of the suborbital borders of the zygoma, (4) slender, angulate zygoma. These characters show that *P. grangeri* is not directly or typically ancestral to the *P. mongoliense* of the Shara Murun formation.

Mandible.—The contrast between the female type jaw, with its small canines (Am. Mus. 20103), and the male jaw of the same species (Am. Mus. 20110) is very marked. In the latter the canines are decidedly larger, the lower lateral incisors, i_3, are not greatly enlarged, the second incisors are somewhat larger, the median incisors are missing; in the same specimen

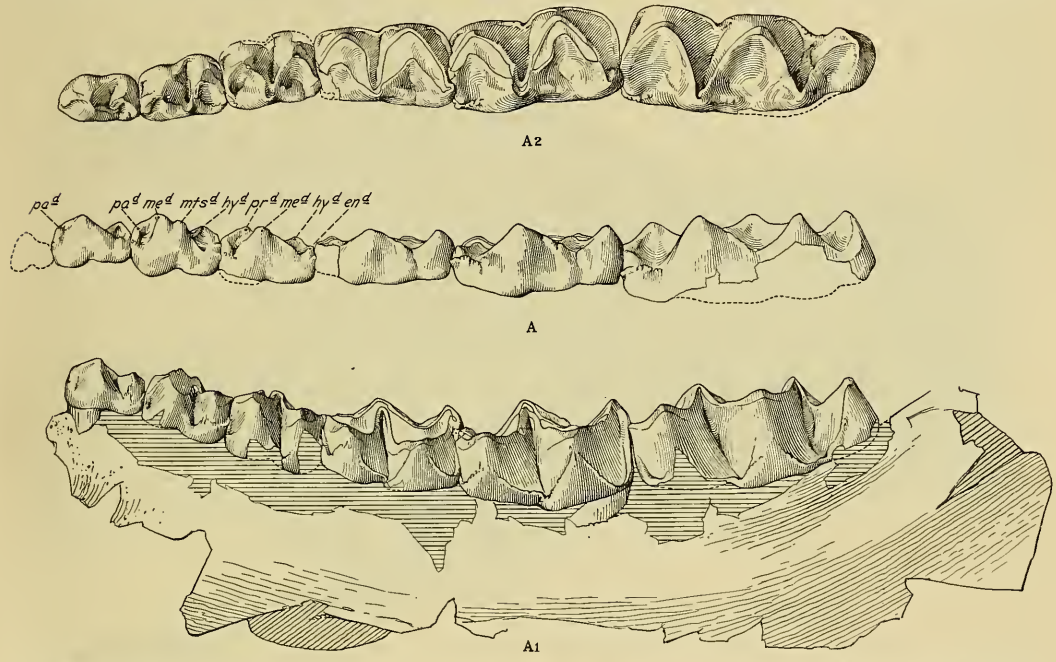


FIGURE 783.—Type right ramus, fragment, with six grinding teeth, of *Protitanotherium mongoliense* Osborn (Am. Mus. 18653), from the Shara Murun formation

A, Internal aspect of type right grinding series, p_2–m_3. Rectigradations indicated as follows: pa^d=paraconid, me^d=metaconid, mts^d=metastylid, hy^d=hypoconid pr^d=protoconid, en^d=entoconid. A_1, External aspect of the type grinding teeth showing relative elevation (hypsodonty) of the crowns and characters of the cingula. A_2, Superior aspect of the type grinding teeth showing relative proportions of the molars and relative development of the talonid or posterior lobe of the premolars. All one-half natural size.

(Am. Mus. 20110) the external sculpturing of the premolars is marked; these teeth are somewhat more hypsodont, and it is possible that we have to do with another species of *Protitanotherium* in the Irdin Manha horizon distinct from *P. grangeri*. Hence the specific reference is entered thus in our table on page 915: "Am. Mus. 20110, *Protitanotherium grangeri?*, referred. Large male jaws with complete dentition."

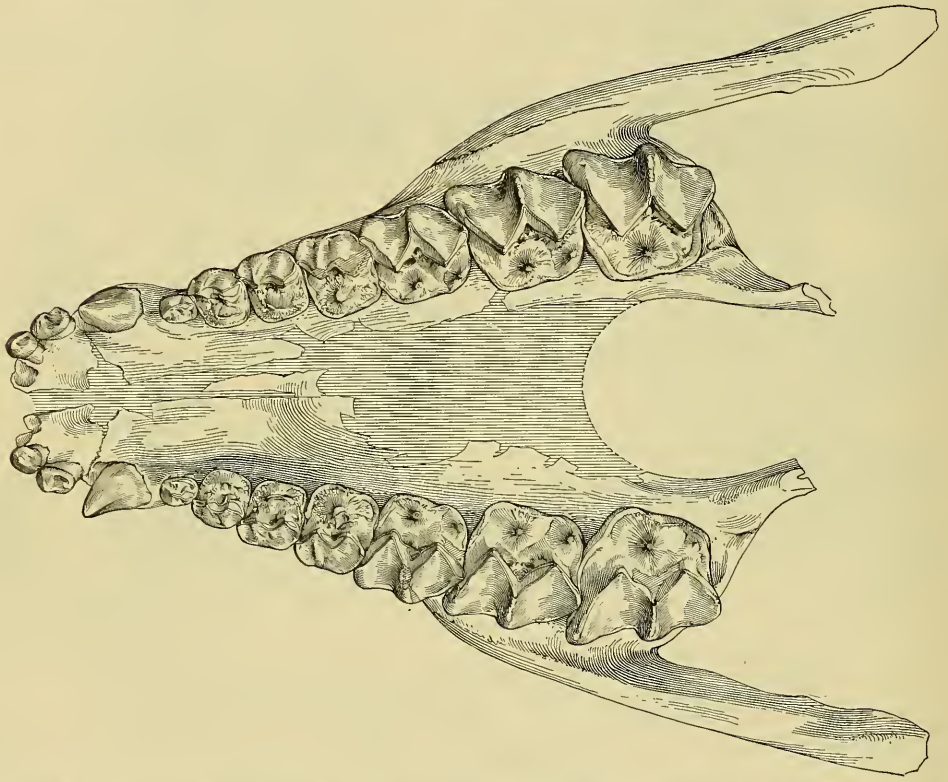


FIGURE 784.—*Protitanotherium mongoliense*, Am. Mus. 20263 (neotype). Palate and complete superior dentition lacking only the median incisor teeth

Observe especially the rudimentary tetartocones in p^{2-3}, the still more rudimentary tetartocone in p^4, the extremely rudimentary hypocone indicated in m^3, particularly in right m^3, as compared with the corresponding rectigradations of the premolar and molar teeth in the less progressive *Protitanotherium grangeri* and in the more progressive *P. andrewsi*. One-third natural size.

Protitanotherium mongoliense Osborn, 1923

Original reference.—Osborn, H. F., Titanotheres and lophiodonts in Mongolia: Am. Mus. Novitates No. 91, October 17, 1923, p. 3.

Type locality and geologic level.—On the Kalgan-Uliassutai trail, near Ula Usu, southeastern Gobi, Mongolia; Shara Murun formation (uppermost Eocene).

Materials.—The materials of this species differ from those referred to *Protitanotherium grangeri* in their occurrence, the specimens having been found close together in a single quarry near the Kaisen quarry, as shown in Figure 770. These very fine materials include the type right ramus, a fragment with six grinding teeth (Am. Mus. 18653); the neotype palate and dentition complete (Am. Mus. 20263); also four referred specimens—Am. Mus. 20256, palate, canine, superior grinders, lower jaws; Am. Mus. 20261, female skull complete but crushed, incisors, canine, grinders; Am. Mus. 20270, right maxilla, zygoma, superior grinders; Am. Mus. 20273, fine pair of jaws lacking symphysis, inferior grinders. These materials agree in their general stage of rectigradations and progression, which is less advanced than that shown in the materials found in the same vicinity and referred to *Protitanotherium andrewsi*.

Specific characters.—The skull, the two palates, the right maxilla, and the two pairs of jaws agree sufficiently with the type jaw in size and in progressive evolution of the incisors, canines, and grinding teeth

clearly to demarcate this species of the Shara Murun from the more primitive *Protitanotherium grangeri* of the Irdin Manha formation. At the same time they indicate a phase of *Protitanotherium* evolution somewhat more ancient geologically than *P. andrewsi*, the giant species of this genus. Unlike *P. grangeri*, the inferior premolars (type Am. Mus. 18653, referred Am. Mus. 20256, 20273) exhibit very distinct entoconids in p_{2-4}, with distinct entoconid shelf and deep talonid basin partly closed internally by the metastylid. Similarly the superior premolars (skull Am. Mus. 20261, referred), palate (Am. Mus. 20256, referred), neotype palate (Am. Mus. 20263), right maxilla (Am. Mus. 20270, referred) all exhibit progressive tetartocones in the second and third premolars, p^{2-3}, and a more or less well-developed tetartocone rudiment in the fourth premolar, p^4. The several maxillae and premolar grinding series show progressive steps in the development of this tetartocone of p^4; in fact, the palatal series (Am. Mus. 20263, shown in fig. 784) exhibits the tetartocones of p^{3-4} in their most rudimentary stage, whereas the tetartocones in the skull (Am. Mus. 20261, fig. 785) are in their most progressive stage.

Hypocone of m^3.—Similar stages of superior molar evolution are observed in the hypocone rectigradation in the four referred specimens of superior grinding teeth: (*a*) the hypocone is not visible in Am. Mus. 20261; (*b*) it is seen in its most rudimentary stage in the right m^3 of Am. Mus. 20263 (figs. 779, 784) whereas (*c*) in the opposite molar, left m^3, of the same specimen, there is exhibited a hypocone no larger than a pinhead.

Dentition.—Of the cutting teeth the male superior canines (Am. Mus. 20263, neotype; 20256, referred) are large and powerful, sharpened at the extremities, obtuse at the base, powerful weapons far surpassing in size the small, recurved canines of the females (skull Am. Mus. 20261, fig. 785). The superior incisors (Am. Mus. 20263, neotype, fig. 790; Am. Mus. 20256, referred) in the males are greatly enlarged, i^3 retaining its supremacy, while i^{2-1} do not exhibit the pointed, incisiform character observed in *Protitanotherium grangeri* but the bluntly rounded character distinctive of American species of *Protitanotherium* and characteristic of all the known American Oligocene titanotheres. Thus the superior canines, premolars, and incisors present marked specific distinctions from *Protitanotherium grangeri*. The inferior incisors, however (Am. Mus. 20256), especially i_{2-3}, exhibit the pointed, typically incisiform character seen in *P. grangeri*, although of nearly double the size.

FIGURE 785.—*Protitanotherium mongoliense*, Am. Mus. 20261, complete female skull, including incisors, canine, and grinders. Collected in the Shara Murun formation

One-sixth natural size. This referred cranium was severely crushed laterally and has been largely restored. It displays the general proportions of the *P. mongoliense* skull and the texture and cream-white color characteristic of the Shara Murun fossils.

Cranium.—The marked cranial distinctions of *Protitanotherium mongoliense* are observed in the skull (Am. Mus. 20261, fig. 785) and palate (Am. Mus. 20263, fig. 784), consisting chiefly of the rounded, simply convex, nonangulate character of the suborbital zygomatic process of the malar; the zygomatic arch, laterally crushed in Am. Mus. 20261, is somewhat broadly expanded; the nasals retain a broad, spatulate, shovel-shaped character; the osseous horns in the females (Am. Mus. 20261, fig. 785) were doubtless smaller than in the males. The mandibular rami, well preserved in the male (Am. Mus. 20256) and probable male (Am. Mus. 20273), are very deep, the

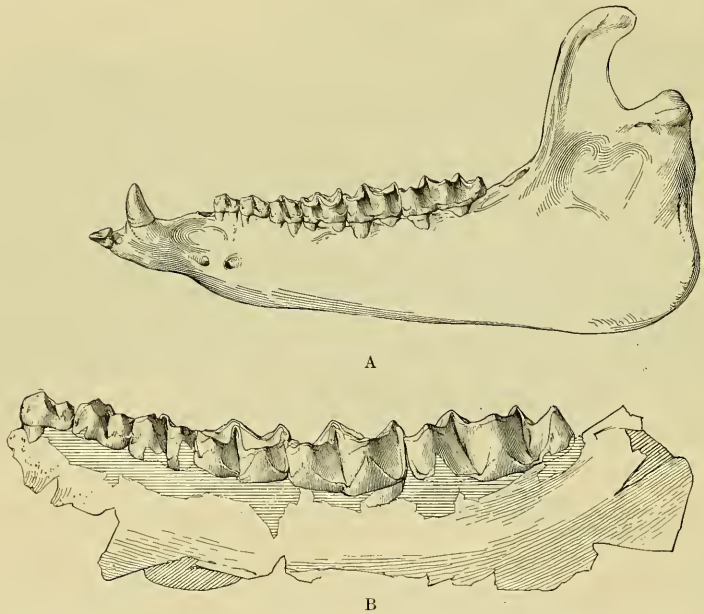
depth being carried forward into the symphyseal region, a characteristic of *Menodus* (= *Titanotherium*); the angular border is depressed, the coronoid is elevated, broadly recurved; the simple, smooth, gently rounded aspects of this jaw enable us to distinguish it readily from the sharply angulate, sculptured, relatively shallow jaw of the *Dolichorhinus kaiseni* type from the same formation, or from the extremely elongate and deepened jaw of the *Telmatherium berkeyi* type from the Irdin Manha formation.

Protitanotherium andrewsi Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Am. Mus. 20254, male skull, superior dentition; Am. Mus. 20262, jaws, symphysis, upper incisors and grinders; Am. Mus. 20269, symphysis of jaws, with canines; Am. Mus. 20280, juvenile palate, deciduous premolars, first and second molars; Am. Mus. 20272, fine jaw, male, inferior dentition. These altogether afford a very complete knowledge of the cranial characters of this species.

Specific characters.—This highly progressive phase of *Protitanotherium* evolution is readily distinguished from the previous ascending mutation of *Protitanotherium mongoliense* by teeth apparently belonging to higher geologic levels of the Shara Murun formation. This advance is indicated not only by the greater measurements of the cranium and jaws throughout,



A

B

FIGURE 786.—Lower jaw of *Protitanotherium andrewsi*, Am Mus. 20272 (A), a finely preserved specimen, for comparison with the imperfect lower jaw of the type of *Protitanotherium mongoliense*, Am. Mus. 18653 (B)

A, one-sixth natural size; B, one-third natural size. Observe the very prominent external cingula on the premolars and molars, especially on m_3, as described in the text; the symphysis is somewhat deformed by downward crushing; the male canines are of very large size.

Type locality and geologic level.—The seven specimens composing the type, paratype, and referred skulls and jaws of this species are from the same geologic locality and level as that which contains the correspondingly abundant remains of *Protitanotherium mongoliense*, yet they exhibit decidedly progressive ascending mutations and rectigradations warranting a specific separation.

Materials.—The type (Am. Mus. 20271), a complete male skull and dentition, nasals wanting; the paratype (Am. Mus. 20251), a supposed male skull, left ramus, and inferior grinders; and five referred specimens—

but by several progressive characters more or less clearly observed in the grinding teeth, although the grinders do not greatly exceed in length those of *Protitanotherium grangeri*.

Dentition.—The dental distinctions are as follows: (1) Tetartocone shelf or spur prominent in p^{2-3}, a distinct tetartocone rudiment (Am. Mus. 20254) or prominent tetartocone spur (Am. Mus. 20271) observed in p^4; (2) similarly faint rudiments of a hypocone in m^3 (Am. Mus. 20271), and a very distinct conical hypocone (Am. Mus. 20254); (3) otherwise the superior grinders, p^1–m^3, exhibit similar characters

to those in *P. mongoliense* and *P. grangeri*; (4) the superior and inferior canines, however, of the males appear to be larger and more robust at the base, not obtuse toward the summit, less lanceolate, more recurved, than in the male canines of *P. grangeri*; (5) the superior incisors exhibit a distinct feature in the relative reduction in size of the lateral incisors, i^3, and in the bluntly rounded summits of the second incisor, i^2 (Am. Mus. 20271), which are similar to those in *P. mongoliense;* (6) the inferior incisors (Am. Mus. 20269) lack this rounded obtuse character of the summits and preserve the pointed postcingulate character seen in *P. mongoliense.*

The inferior premolars (Am. Mus. 20271, type; 20272, referred) present a slight but distinct progression of the entoconids, metastylids, and valleys of the talonid upon the *P. mongoliense* stage. The external sculpturing of the inferior premolars and molars is very marked; the cingulum stands out prominently in the premolars and very prominently in the molars, especially in m_3 (Am. Mus. 20272, referred; 20271, type); this cingulum prominence distinguishes *P. andrewsi* from its ancestor *P. mongoliense* of the Shara Murun and very distinctly from the more ancient *P. grangeri.*

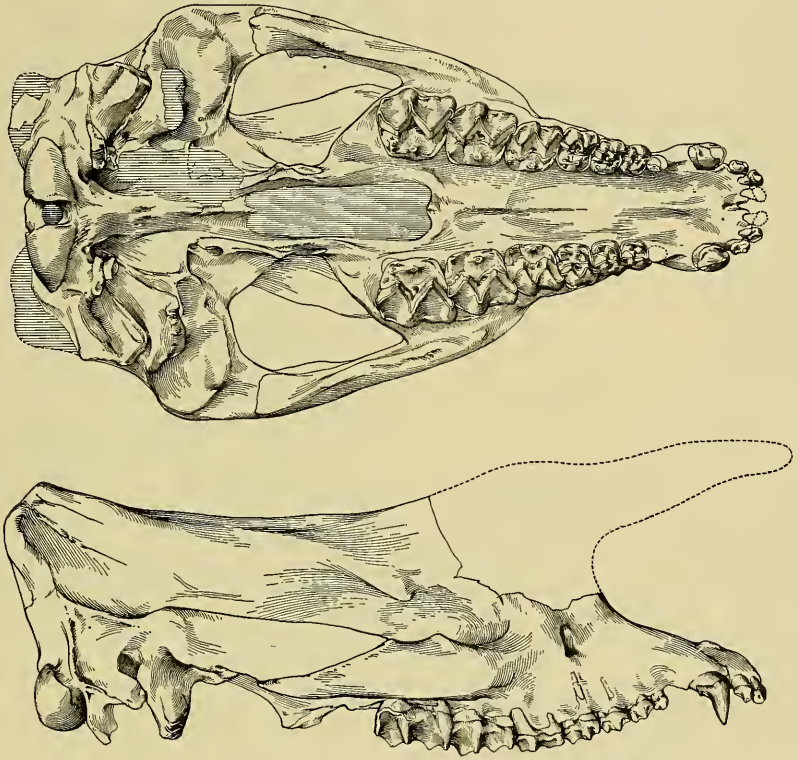


FIGURE 787.—Type cranium of *Protitanotherium andrewsi* Osborn (Am. Mus. 20271), Shara Murun formation

One-sixth natural size. This large male cranium lacks the anterior frontonasal region. The large canines are thoroughly characteristic of the species. Observe the distinct development of the tetartocones in p^4, also the small hypocones in m^3.

Skeletal remains referred to Protitanotherium grangeri, P. mongoliense, and P. andrewsi

Skeletal material is rare in the Irdin Manha formation, but we may with some confidence refer to *Protitanotherium grangeri* (Am. Mus. 20171, belonging to more than one individual) portions of the right and left fore limbs including both the ulno-radii, one humerus, one tibia, and an axis, which display the measurements shown on page 932 in comparison with referred *P. mongoliense* and *P. andrewsi.*

Measurements, in millimeters, of skeletal remains referred to Protitanotherium

	Limb skeleton (Am. Mus. 20171) referred to P. grangeri[a]	Hind limb skeleton (Am. Mus. 20277) referred to P. mongoliense[b]	Incomplete hind foot (Am. Mus. 20274) referred to P. mongoliense[a]	Limb skeleton (Am. Mus. 20327) referred to P. andrewsi[a]
Articular length of radius	400	(?)	(?)	(?)
Articular length of ulna	398	(?)	(?)	(?)
Estimated articular length of humerus	400	(?)	(?)	454
Articular length of tibia	350	400	(?)	(?)
Articular length of femur	(?)	650	(?)	(?)
Articular length of fibula	[c] 330	380	(?)	(?)
Total length of calcaneum	(?)	163	(?)	(?)
Total width of astragalus	(?)	92	(?)	(?)
Total length of median metatarsal	(?)	175	189	(?)
Combined articular length of humerus and ulno-radii in limb referred to P. grangeri	[c] 700	(?)	(?)	(?)
Total height of hind limb, femur, tibio-fibula, pes		1, 400		

[a] Belonging to more than one individual.
[b] Belonging to one individual.
[c] Estimated.

Protitanotherium grangeri.—The tibia is also short in this specimen of *P. grangeri* (Am. Mus. 20171, belonging to more than one individual), the articular length being about 350 millimeters (1 foot 2 inches), as compared with an articular length of about 400 millimeters (1 foot 3½ inches) in a specimen (Am. Mus. 20277, belonging to one individual) referred to *Protitanotherium mongoliense.*

Protitanotherium mongoliense.—The left hind limb of one individual referred to *P. mongoliense* (Am. Mus. 20277), including femur, patella, tibia, and complete tarsus, has a length of 1,400 millimeters (4 feet 7 inches) when completely stretched out. The three metatarsals are rather slender, the median one, Mts III, having a complete length of 7 inches, whereas the median metacarpal (*P. mongoliense?*, Am. Mus. 20274, more than one individual) has a median articular length of 7½ inches. Am. Mus. 20277 (one individual), in which the superior articular length of the femur is 650 millimeters (2 feet 2 inches) and the articular length of the tibia about 400 millimeters (1 foot 3½ inches), is distinctly titanotheroid.

A manus (Am. Mus. 20258) has a median metacarpal articular length of 18 millimeters, such as we should naturally attribute to the manus of *P. mongoliense.*

Protitanotherium andrewsi?.—The series of larger associated metapodials of one individual from the Shara Murun formation bears the number Am. Mus. 20259 and, although abbreviated at the distal extremities, so far surpasses in size the measurements of *P. mongoliense?* (Am. Mus. 20274) that it may be attributed to the larger species *Protitanotherium andrewsi.* The massive humerus (Am. Mus. 20327) found in the Shara Murun formation has an articular length of 454 millimeters (1 foot 6½ inches). It is distinctly titanotheroid in structure, with very broad, high, bicipital crest. This large humerus also may well belong to the more progressive species *P. andrewsi.*

Pro-Menodus phylum sp.?.—In the Shara Murun formation occurs also an extremely long, slender-limbed species of animal represented by a femur (Am. Mus. 20253). This femur is actually as long (680 mm.) as that referred above to *Protitanotherium mongoliense* (Am. Mus. 20277), but it is far more slender—in fact, too slender to belong to any known species of titanotheres unless it be to the line of the ancestral slender-limbed *Menodus.* With it is a long, slender right ulna (402 mm.) and a number of slender spine dorsal vertebrae, a lunar, and one metapodial. If compelled on this meager evidence to place this species in its proper phylum, we should be inclined to describe it as an ancestral form of the *Menodus mongoliensis* of the Ardyn Obo formation. The ulna is much less elongate than in the long, slender-limbed ancestors of *Baluchitherium.* A tibia of similarly long, slender proportions (Am. Mus. 20327B) may represent a long-limbed titanothere of the *Menodus* rather than of the robust *Brontops* type.

There are other remains of the limb skeleton from the Shara Murun formation—part of the pes (Am. Mus. 20274), foot bones (Am. Mus. 20327a, b, c, d, etc.)—which must await specific determination until further evidence is afforded by additional material.

Conclusion.—On comparing the above measurements and preliminary description of the limbs of *Protitanotherium grangeri, P. mongoliense,* and *P. andrewsi,* we observe a progressive increase in length and in massiveness which is harmonious with the progressive increase in size of the crania of these three species of titanotheres.

In these, as in the American titanotheres, the humerus and ulno-radius are subequal in length and the femur is relatively much longer than the tibio-fibula. These proportional measurements again agree closely with those found in the American titanotheres.

SUBFAMILY TELMATHERIINAE

Telmatherium Marsh, 1872

Generic characters.—The generic characters of this deep-jawed Mongolian titanothere are inferred only from the gigantic type jaw and inferior and superior dentition of *Telmatherium berkeyi* and of six other specimens discovered in the Irdin Manha formation. As the entire upper and posterior portion of the

cranium is unknown, no direct comparison can be made with either *Dolichorhinus* or *Protitanotherium;* yet from the extreme depth of the jaw in comparison with American species we may be confident that the skull was relatively high and deep as well as long. lower borders. The incisors are the largest known among the titanotheres, especially the second pair. The canines are very large and pointed—sublanceolate. The premolars have prominent crowns and highly sculptured internal cingula. The posterior

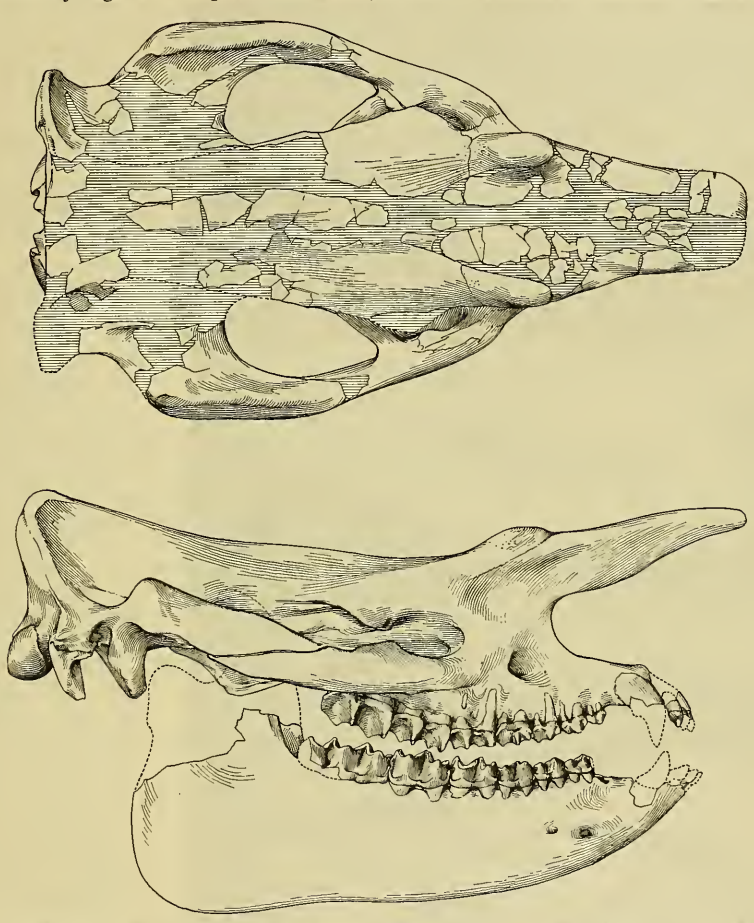


FIGURE 788.—Referred cranium and jaw of *Protitanotherium andrewsi;* cranium (Am. Mus. 20254), paratype jaw (Am. Mus. 20251)

One-sixth natural size. This composition of male cranium and jaw exhibits the elongate frontonasal horns and the long shovel-shaped nasals characteristic of *Protitanotherium.* To correct the crushing of the parieto-occipital crest in the original specimen the occiput has been raised after the manner of *Protitanotherium.* The crushed premaxilla is also restored. The jaw (Am. Mus. 20251) is reversed from the left jaw of the opposite side. The superior view of this cranium shows the extensive restoration and the placing of the crushed fragments in their approximate position; it also illustrates the saddle-shaped broadening of the top of the cranium between the lambdoidal crests, and the rounded, elongate frontal horns resting upon the nasals.

In the American species the bony horns are very rudimentary and the canine tusks are sharp and powerful. The jaws contrast widely with those of *Dolichorhinus* and of *Protitanotherium* not only in their prodigious size but in the great depth of the mandibular rami, of the chin processes, and of the molars are exceptionally long and relatively narrow, the breadth-length index being 82 as compared with 98 in *Dolichorhinus* and 115 in *Brontops brachycephalus.*

Certainly the habits and probably also the habitat of *Telmatherium* differed widely from those of either *Dolichorhinus* or *Protitanotherium.*

Telmatherium berkeyi Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

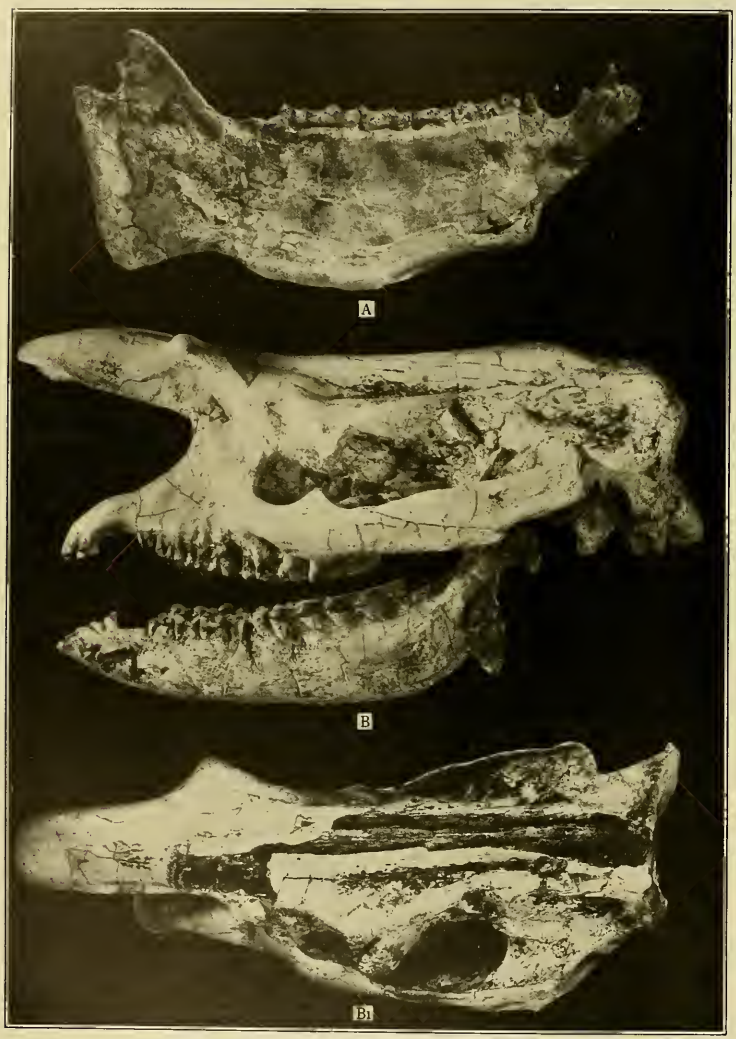


FIGURE 789.—Types of *Telmatherium* and of *Dolichorhinus* from the Irdin Manha and Shara Murun formations

A, Type female jaw of *Telmatherium berkeyi* (Am. Mus. 20106), one-eighth natural size; B, cranium of *Dolichorhinus kaiseni* (Am. Mus. 20252), left lateral aspect, after restoration, one-sixth natural size; B_1, superior view of same cranium (Am. Mus. 20252), showing the tubular cavities lying beneath the cranial surface, as exposed before complete restoration of the top of the skull, one-sixth natural size.

Type locality and geologic level.—The type of *Telmatherium berkeyi* (Am. Mus. 20106), consisting of adult female lower jaws, right maxilla, canines, and grinders, and the paratype (Am. Mus. 20107), anterior half of jaw, canine, and inferior grinders, are both from the Irdin Manha formation, 1 mile south of the Kalgan-Urga telegraph line. This locality yielded also the palate and superior grinders (Am. Mus. 20127) and the juvenile lower jaw with incisors and grinder (Am. Mus. 20115). The other paratype (Am. Mus. 20121), a perfect left maxilla with grinding teeth, comes from the same formation but from a locality 2 miles north of the Kalgan-Urga telegraph line.

Materials.—The materials referable to *Telmatherium berkeyi*, listed in the table on page 915, were discovered at three localities north and south of the Kalgan-Urga telegraph line, in the Irdin Manha formation. They consist of seven specimens altogether, found in association with remains of *Protitanotherium grangeri*. This fact would indicate that although *T. berkeyi* was a much larger and probably a longer-limbed form and had different feeding habits, it frequented the same general region as *P. grangeri*. This inference is in accord with the fact that *Telmatherium* and *Manteoceras* occur in northern Utah in similar geologic formations, although they probably occupied a dissimilar local habitat.

General characters.—As indicated in the generic analysis of *Telmatherium* above, one could not for a moment mistake the extremely deep-jawed, bathygnathic *Telmatherium berkeyi*, with deeply depressed mental region or chin, for its relatively shallow-jawed contemporary *Protitanotherium grangeri* or for its extremely shallow-jawed contemporary *Dolichorhinus olseni*. In fact, the elongate jaw of *T. berkeyi*, measuring 30 inches from condyle to symphysis, nearly 9 inches in its deepest portion below m_2, m_3, and 7½ inches

at the symphysis, is quite unique; it betokens a long, deep cranium of prodigious size. Unlike that of its contemporaries, the coronoid is very broad; the condyle is only moderately elevated above the line of the molar teeth; the angle is small, not prominent; the lower border is deeply depressed below the grinding series, then rises slightly below the premolars and sinks into the deep, powerful symphysis, which rises like the inclined straight prow of a ship to the elevated border of the cutting teeth. These mandibular characters are clearly displayed in the type (Am. Mus. 20106) and in the paratype (Am. Mus. 20107). The extremely juvenile pair of jaws (Am. Mus. 20115) with its series of milk teeth displays only the swelling beneath the molars and the very peculiar straight or slightly concave chin.

The cranial parts preserved above the maxillary dental series display a highly characteristic flattened suborbital malar region, wholly different from the angulate or rounded malar region of *Protitanotherium* or of *Dolichorhinus*. Consequently we await with great interest a fuller knowledge of the cranium of this large and peculiar animal, feeling quite confident that it will display on a titanic scale characters similar to those of *Telmatherium ultimum*, last known of the titanotheres of this phylum in America. Like *T. ultimum*, it shows many signs of affinity with the true dolichocephalic *Menodus* (= *Titanotherium*) *giganteus* of North America. These resemblances to *Menodus* in the deep rami and deep chin are only partly sustained by the characters of the cutting and of the grinding teeth.

Dental characters.—The cutting teeth are all extremely prominent. The superior canines in the males are like those of *Telmatherium* and of *Menodus* (= *Titanotherium*) in their prominent size and in their laterally compressed crowns with trenchant edges

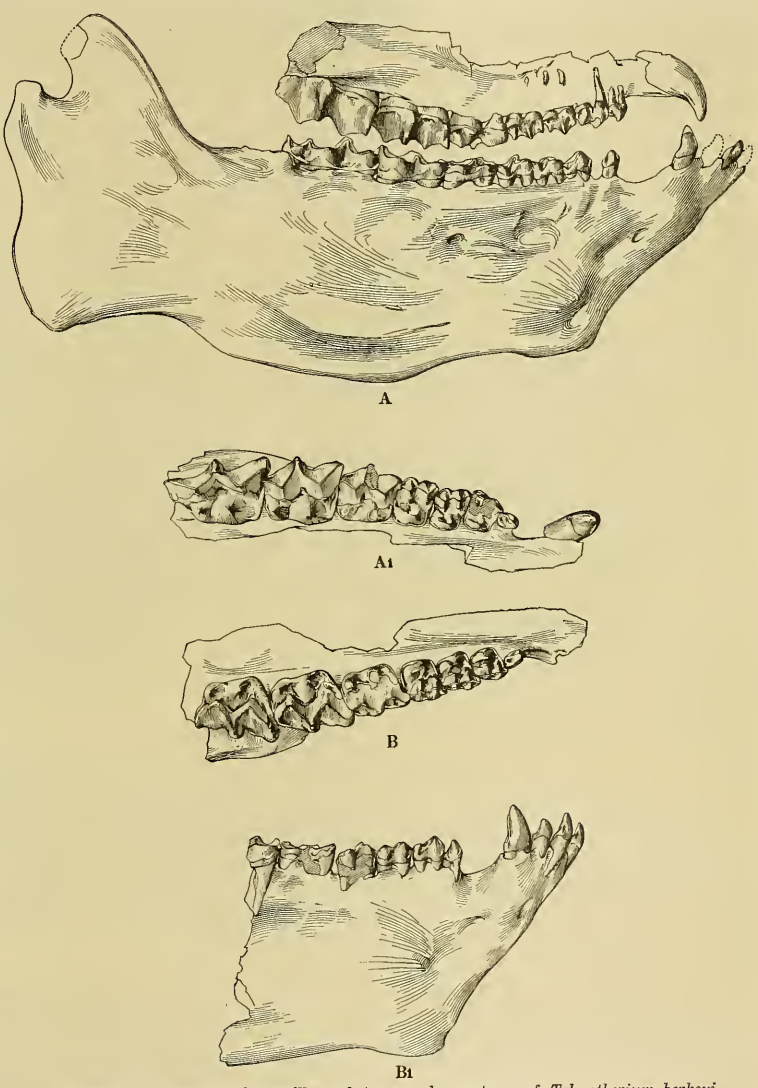


FIGURE 790.—Jaws and maxillae of type and paratype of *Telmatherium berkeyi*, Irdin Manha formation (upper Eocene)

A, Type maxilla and lower jaw of a female individual (Am. Mus. 20106), lateral view. A1, Crown view of type superior premolar-molar grinding series (Am. Mus. 20106). B, Crown view of paratype superior premolar-molar grinding series (Am. Mus. 20121). Observe that the paratype grinders are somewhat more progressive than the type grinders in the development of the tetartocones in the premolars, also in the deep invaginations anterior to the ectolophs in the molars. B1, Lateral aspect of the paratype male jaw (Am. Mus. 20107). Observe the deep symphysis, the straight, upward anterior border of the symphysis, the enlarged male canines, and the enlarged male incisors. All one-sixth natural size.

extending to the base, facing internally, a similarity due to relationship to or convergence with *Menodus*. The marked incisive distinction from *Protitanotherium* is that the lateral incisors ($I\frac{3}{3}$) are smaller than the second incisors ($I\frac{2}{2}$) and even somewhat smaller than the median incisors ($I\frac{1}{1}$). All the incisors are very prominent, flattened anteroposteriorly, not deeply cupped behind, gently postcingulate.

High laterally compressed inferior premolar series with highly sculptured crowns, a flattened p_1, a highly flattened p_2 with shallow talonid basin, a somewhat broader p_3 with broad talonid basin, a still broader p_4 with talonid basin broader than that of the trigonid. These characters clearly distinguish the premolar teeth from those of both *Dolichorhinus* and *Protitanotherium*—in fact, the lower premolars are wholly different. The same is true of the laterally compressed superior premolars with prominent sculptured ectolophs, laterally compressed deuterocones with very feebly indicated rudiments of tetartocone ridges and without distinct tetartocone prominence.

Harmonic with these laterally compressed premolars are the extremely elongate, laterally compressed molar teeth, the narrowest teeth of the kind to be seen among the titanotheres, distinguished by two deep concavities between the ectoloph and the inner portion of the crown, these depressions reminding us of those developed in a few of the Oligocene titanotheres. On the inner side of these narrow crowns lie fairly prominent protocones and hypocones. In m^3 there is a trace of a protoconule and the narrow posterointernal shelf of the crown bears a very prominent hypocone, a relatively rare feature in titanotheres and very distinctive as compared with the absence of a hypocone in m^3 in both *Protitanotherium* and *Dolichorhinus*.

The above dental characters are displayed in the second paratype specimen (Am. Mus. 20121) belonging to a more aged individual; also in a more progressive individual wherein we observe in the superior premolars tetartocones increasing in prominence and in distinctness as we pass from p^2 to p^4, a progressive feature of premolar development not observed in either of the other Irdin Manha species. A third maxilla (Am. Mus. 20106), associated with the type jaw, displays a more rudimentary condition of the tetartocones in the third superior premolars.

Consequently among the materials referable to this genus and species we observe several stages of progressive development in the evolution of the superior and inferior premolar teeth.

SUBFAMILY BRONTOPINAE

Brontops Marsh, 1887

Generic characters.—The generic characters of this broad-headed Mongolian titanothere are not readily derived from the badly crushed skull, symphysis of lower jaw, and single lower molar found in the Ardyn Obo formation, of lower Oligocene age. The cranial proportions are short and broad; the robust, widely arched zygomatic arches are correlated with strong powers of mastication; the breadth-length index of 74, estimated from the reconstructed skull (length 576 mm., breadth 424 mm.—actual 500 mm.), contrasts with the index of 58–69 in the widely arched *Protitanotherium* and of 47 in the narrowly arched *Dolichorhinus*. The cranium is actually much shorter than that of either *Dolichorhinus* (660–695 mm.) or *Protitanotherium* (695–757 mm.). The horns partake of the short, broad character of the cranium; they are obtusely prominent. The elongated nasals are broad and shovel-shaped, as in *Protitanotherium* and *Titanotherium*. The symphysis of a referred jaw is extremely massive, like that of *Brontops*. The dental formula, $I\frac{3-3}{3-3}$, $C\frac{1-1}{1-1}$, $P\frac{4-4}{4-4}$, $M\frac{3-3}{3-3}$, agrees with that of *Teleodus* Marsh in the presence of three superior incisors and differs from that of *Brontops brachycephalus* Osborn, in which the incisive formula is $I\frac{2-2}{2-2}$. The cranium is as brachycephalic as that of *Brontops brachycephalus*, as shown in the full description of *B. brachycephalus* above. The strong, well-developed tetartocones of the premolars or double internal premolar cones mark the chief progression beyond *Protitanotherium*. Most of the measurements in the following table are estimates, as the skulls were crushed.

Measurements of Brontops gobiensis and B. brachycephalus, in millimeters

	B. gobiensis, Am. Mus. 20354 (type)	B. brachycephalus, Am. Mus. 1495 (referred)
Basilar length of skull (anteroposterior)	[a] 576	570
Transverse zygomatic width	[a] 424	[a] 337
Breadth-length or cranial index	[a] 74	----
P^2–m^3	300	286–291
M^3, anteroposterior	72–78	61
M^3, transverse	64–70	68–70
M^3, index	82	111–115

[a] Estimated.

Brontops gobiensis Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type description (Osborn, 1925, p. 5).—"In the Ardyn Obo formation were found remains of three titanotheres in a distinctly Oligocene stage of evolution. The type skull (Am. Mus. 20354), named herewith *Brontops gobiensis*, contains three superior incisors with distinct tetartocones in the three molars; no hypocone in m^3. The massive symphysis (Am. Mus. 20353) is referred to the same species."

Type cranial characters.—The type skull is extremely crushed and flattened; the upper facio-cranial portion is distorted to the left, the maxillary portion is distorted to the right. This distortion is corrected in the reconstructed figure (fig. 791). The free portions of the nasals measure (ap. by tr.) 169 by 142 millimeters; cephaly; the occipital condyles measure 150 millimeters transversely. The hard palate opens into the posterior nares between m^2, m^3.

Below the incisive border three small alveoli may be detected on each side, both crowns and fangs being wanting; the incisors were probably partly vestigial.

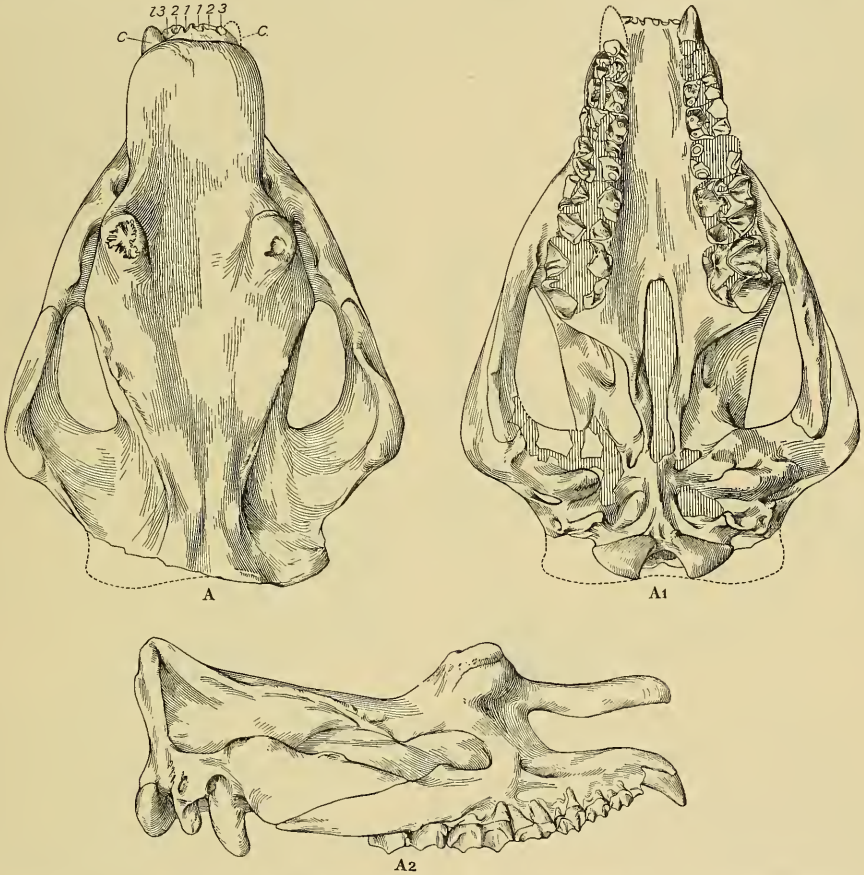


FIGURE 791.—Cranium and superior dentition of the type of *Brontops gobiensis* (Am. Mus. 20354, cranium reconstructed after comparison with that of *Brontops brachycephalus*)

A, Cranium in superior aspect. Observe the extraordinarily broad proportions, the indented summits of the horn cores, the protrusion of the incisive borders indicated by the alveoli of the six incisors. A1, Palatal view of the type specimen showing the same broad proportions of the cranium; also the reduplication of the premolar cones, deuterocones, and tetartocones, as well as the absence of a hypocone. A2, Right lateral view of the same cranium, displaying the horn cores in lateral aspect, the nasals relatively longer than in *B. brachycephalus*, and the absence of a postcanine diastema. All one-sixth natural size.

they are both long and broad. The bony horns rise gradually directly above the orbits from a sloping base (119 mm.) to a height of 53 millimeters and to a width of 57 millimeters. The cranial vertex narrows to 80 millimeters between the temporal fossae. The occiput is low and broad, in harmony with the general brachy-

The approximate measurements of the left canine are, base, anteroposterior 33 millimeters, transverse 25, height of crown 43 (estimated)—obviously a short, obtuse canine.

Of the superior premolars, p^1 is very small (ap. 18 mm., tr. 15); p^2 (ap. 26 mm., tr. 33, estimated)

exhibits a rudimentary tetartocone spur; p^3 (ap. 29 mm., tr. 41) exhibits a prominent and distinct tetartocone; p^4 (ap. 34 mm., tr. 51, estimated) has a prominent and distinct tetartocone.

The partly crushed molars, m^{1-3}, measure 208 millimeters on the left side, probably elongated but crushed; the approximate proportions are, m^2, anteroposterior 74 millimeters, transverse 64, with subequal protocone and hypocone, ectoloph slightly cingulate; m^3, anteroposterior 80 millimeters, transverse 72 (estimated), without hypocone, a prominent cingulate shelf.

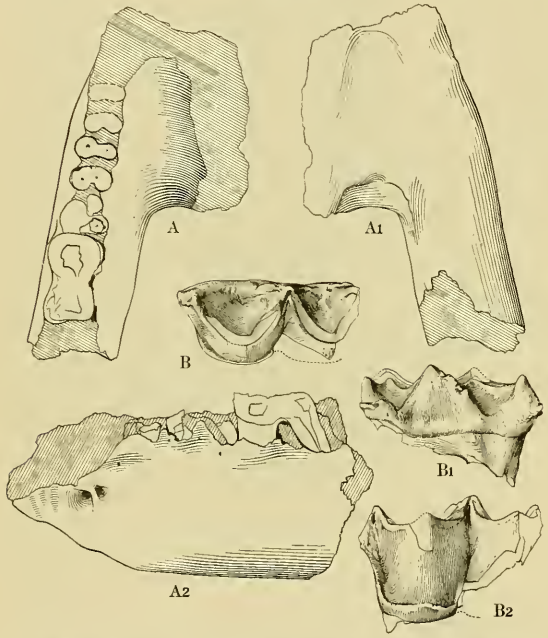


FIGURE 792.—Referred jaw of *Brontops gobiensis* (Am. Mus. 20353) and type right second lower grinding tooth of *Menodus mongoliensis* (Am. Mus. 20351)

Jaw one-fourth natural size, grinding tooth nine-eighths natural size. A, Superior aspect of referred symphysis of *Brontops gobiensis;* A_1, inferior aspect of same symphysis; A_2, left lateral aspect of same symphysis; B, superior aspect of type right second lower grinding tooth of *Menodus mongoliensis;* B_1, internal aspect of same tooth; B_2, external aspect of same tooth.

Other type characters and measurements may be derived from Figure 791 and from the occiput as figured in Figure 775, A.

Comparison with Brontops brachycephalus.—The type cranium of *Brontops gobiensis* indicates an animal of approximately the same size as the larger specimens of South Dakota referable to *Brontops brachycephalus,* namely, Am. Mus. 1495 and Am. Mus. 4259.

The skull of *B. gobiensis* of Mongolia is less progressive than that of the American *B. brachycephalus* in retaining the extremely elongate, shovel-shaped nasals characteristic of *Protitanotherium;* also in the elongation of the bases of the horn cores. *B. gobiensis* is also conservative in retaining three incisors above, as in the upper Eocene American and Mongolian species of *Protitanotherium. Brontops gobiensis* is progressive and allies itself with the American species of *Brontops* in its extreme brachycephaly. The tetartocones in the superior premolars (p^1, p^2, p^4) of *B. gobiensis* are decidedly more progressive than those in the referred skull of *B. brachycephalus* (Am. Mus. 4259). Consequently, although we regard *B. gobiensis* as more nearly referable to the genus *Brontops* than to any other genus of American titanotheres, it is clearly distinguishable from members of the *Brontops* phylum beginning with *B. brachycephalus* and ending with *B. robustus,* of the upper titanothere-bearing beds (Chadron formation) of South Dakota.

Referred jaw and symphysis (Am. Mus. 20353, fig. 792, A, A_1, A_2).—A jaw from the Ardyn Obo formation, collected in 1923, is somewhat doubtfully referred to the species *Brontops gobiensis,* because it is extremely massive and because the incisive, canine, and anterior premolar borders are poorly preserved. The approximate measurements are:

	Millimeters
Length of symphysis	146
Width of symphysis	170
Depth of symphysis	84
Width of ramus	67

Other characters of this jaw are clearly displayed and figured in Figure 792.

SUBFAMILY MENODONTINAE

Menodus Pomel, 1849

The generic characters of this long-headed titanothere as it appeared in Mongolia are derived from the single type molar tooth discovered in the Ardyn Obo formation, of lower Oligocene age. In contrast to that of *Brontops,* this tooth is long and narrow and has elevated or hypsodont crowns, prominent highly sculptured cingula, sharp serrate ridges descending from the internal cusps, broadly open valleys of the trigonid and of the talonid. This form of lower grinding tooth, which constitutes the type of *Menodus mongoliensis,* belongs with an elongated cranium, an elongated grinding series, deep, narrow mandibular rami, deep and not broadly expanding zygomatic arches, and elongate and relatively slender limbs and feet—a harmonic group of cranial, dental, and skeletal characters as far as possible from the *Brontops* form.

The existence of a species of the genus *Menodus* in central Asia is apparently confirmed by the presence of a related species discovered in Bohemia, namely, *Menodus* (= *Titanotherium*) *bohemicus* Kiernik.

Menodus mongoliensis Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type locality and geologic level.—The type of *Menodus mongoliensis* is from the Ardyn Obo formation, *Brontops gobiensis* life zone, collected on the Kalgan-Uliassutai trail, southeastern Gobi, Mongolia.

Specific characters.—The type of *Menodus mongoliensis* (Am. Mus. 20351) is a second right inferior molar in which the second lobe is perfect and the first lobe is broken in front. This fractured molar (fig. 792, B, B_1, B_2) corresponds best in size and character with the two lobes of the second inferior molar of the right side, of a large male of *Menodus* (= *Titanotherium*) *giganteus* of the lower Oligocene Chadron formation (horizon B) of South Dakota; in fact, these lobes exceed in length those of the largest specimens of the true female *Menodus giganteus* in the American Museum collection. Consequently, we refer this tooth not to any species of *Brontops*, in which the second lower molars are relatively broad, low-crowned, and less elongate anteroposteriorly, but to a gigantic species of *Menodus*, to which the name *Menodus mongoliensis* has been provisionally assigned. The specific characters are as follows:

A large menodont equal in size to the largest *Menodus giganteus* of South Dakota; second inferior molars relatively elongate, narrow, with elevated crowns. Estimated length of two lobes 93 millimeters, as compared with 83 millimeters in a large female *Menodus giganteus* (Am. Mus. 506), and also as compared with the corresponding measurement of 80 millimeters of the two lobes of m_3 in Marsh's type of *Brontops robustus*. The width of the anterior lobe of this type molar of *M. mongoliensis* is 40 millimeters, as compared with a width of 52 millimeters in the corresponding lobe of *B. robustus* and of 42 millimeters in *M. giganteus* (Am. Mus. 1007). Height of unworn second lobe 53 millimeters. Other specific characters are the elevation or subhypsodonty of the anterior lobe (53 mm.) prominent postero-external cingulum; also elevated and serrated crest extending backward from the metaconid; prominent posterior cingula on metaconid and hypoconid; internal valleys of trigonid and talonid widely open, shallow character of the internal valleys; molar proportions similar to those of *Menodus*, indicating a long-headed rather than a broad-headed animal.

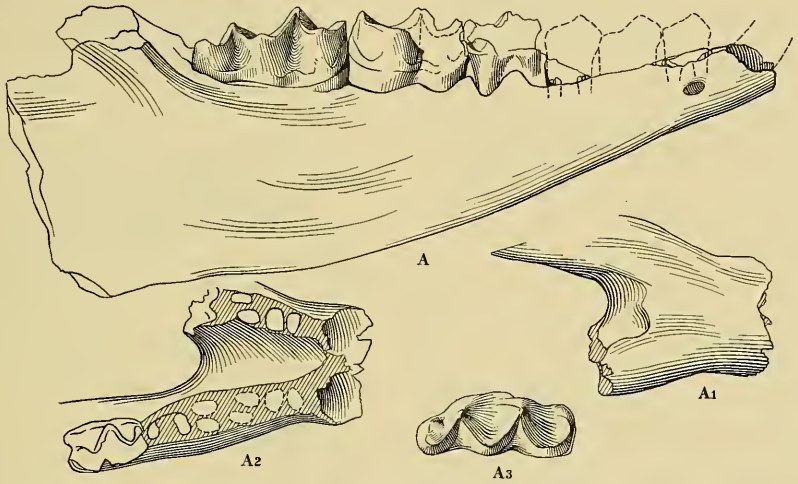


FIGURE 793.—Type jaw of *Manteoceras? irdinensis* (Am. Mus. 20111), Irdin Manha formation (upper Eocene)

A, Right lateral aspect of jaw with crowns of premolar teeth and canine teeth restored in outline; A_1, inferior aspect of symphysis of same specimen; A_2, superior aspect of symphysis and alveoli of anterior teeth; A_3, superior aspect of third inferior molar. All one-third natural size.

MONGOLIAN TITANOTHERES OF UNCERTAIN GENERIC REFERENCE

SUBFAMILY MANTEOCERATINAE (BRONTOPINAE)

Manteoceras Hatcher-Wortman, 1895

The species described herewith as *Manteoceras? irdinensis* is of doubtful generic reference to the "prophet-horned" genus *Manteoceras*, so highly characteristic of the upper levels of the Bridger formation of the Bridger and Washakie Basins of Wyoming and of levels A and B of the Bridger formation of the Uinta Basin of Utah. The type jaw (Am. Mus. 20111), from the Irdin Manha formation of Mongolia, is a titanothere clearly distinguishable both specifically and generically from other Irdin Manha species; it certainly does not belong either to *Protitanotherium* or to *Dolichorhinus*. Although on the whole it pre-

sents a nearer resemblance to the American *Manteoceras*, it probably represents a distinct genus of titanotheres or of chalicotheres characterized by procumbent lower canine teeth.

Manteoceras? irdinensis Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type locality and geologic level.—The type jaw (Am. Mus. 20111) of *Manteoceras? irdinensis* is from the Irdin Manha formation, 2 miles north of the Kalgan-Urga telegraph line. It includes the greater part of the right ramus, containing the three true grinding teeth, m_{1-3}. The premolar alveolar border is partly fractured, and it is difficult to determine the number or form of the premolar teeth. A highly distinctive character is the broad, flattened symphysis, containing two very large alveoli, apparently for a pair of approximated, procumbent canine teeth; the enlarged canines leave only a narrow space for the incisive border. The imperfect condition of the specimen prevents our determining the formula of the cutting teeth. The principal characters in profile, superior, and inferior views are clearly shown in the type (fig. 793), in which the supposed outlines of the premolar teeth are properly restored.

Principal measurements of Manteoceras? irdinensis

	Millimeters
Grinding series, $?p_2$–m_3	270
Premolar series	80
Molar series	190
M_1, ap. by tr. (index 64)	42×27
M_2, ap. by tr. (index 50)	60×30
M_3, ap. by tr. (index 40)	83×33
Transverse measurement of two inferior canine alveoli, outer sides	58
Length of inferior symphysis, estimated	88
Depth of symphysis from median point	36

Specific characters.—(1) Symphysis of mandibular ramus broad, shallow, flattened inferiorly, containing alveoli for two enlarged semiprocumbent canines; (2) space occupied by premolars relatively reduced (80 mm.), as in all titanotheres, p_1 apparently absent or vestigial; (3) true grinders, m_{1-3}, rapidly increasing in anteroposterior diameter (190 mm.), a characteristic titanotheroid feature; (4) faint sculpturing of the external cingula in the outer valleys only, extending over the outer lobes; (5) ramus deepening to 119 millimeters behind m_3. The ramus, as preserved, is 400 millimeters long, being greatly inferior in proportions and length to the ramus of *Protitanotherium grangeri*.

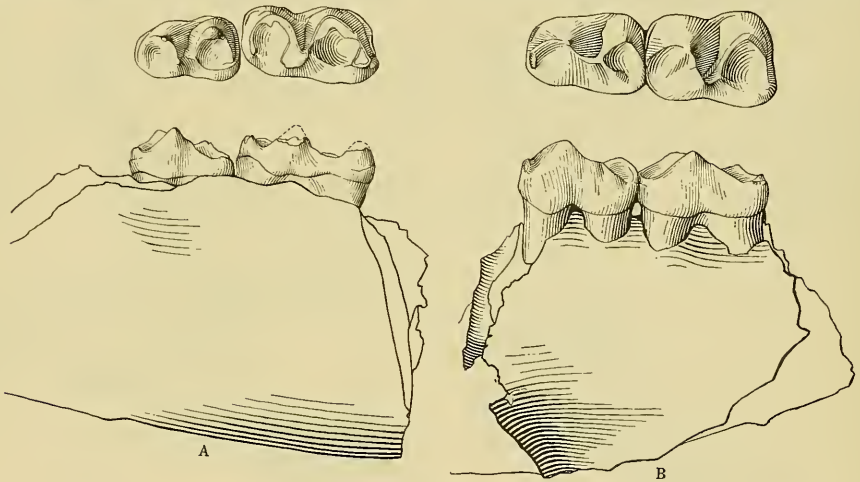


FIGURE 794.—Type jaw (fragment) of *Metarhinus? mongoliensis* (Am. Mus. 20167), compared with *Protitanotherium grangeri* (Am. Mus. 20168)

Natural size. (Compare fig. 774, G). A, Superior and lateral aspects of fourth inferior premolar and of first inferior molar of *Metarhinus? mongoliensis* (Am. Mus. 20167) from the Irdin Manha formation; B, lower jaw fragment, p_4, m_1, of *Protitanotherium grangeri* (Am. Mus. 20168) from the Irdin Manha formation.

SUBFAMILY DOLICHORHININAE

Metarhinus Osborn, 1908

The fragmentary type jaw here described as *Metarhinus? mongoliensis* (Am. Mus. 20167) certainly represents a species of titanothere distinct from any previously described from Mongolia in this monograph, as it is separated from all others both by its diminutive size and by the peculiar form of the two lower grinding teeth preserved (p_4?, m_1). Comparison with all the known specimens of chalicotheres and titanotheres of corresponding age shows that it most nearly resembles the small titanothere known as

Metarhinus, an animal highly characteristic of the fluviatile deposits of levels A and B (Bridger formation) of the Uinta Basin, Utah. The reference to *Metarhinus*, however, is still very doubtful, so that for the generic reference of this jaw, as for that of the imperfect jaw referred to *Manteoceras*, we must await the evidence that may be afforded by more perfectly preserved material.

Metarhinus? mongoliensis Osborn, 1925

Original reference.—Osborn, H. F., Upper Eocene and lower Oligocene titanotheres of Mongolia: Am. Mus. Novitates No. 202, 1925.

Type locality and geologic level.—The type jaw (fragment) of *Metarhinus? mongoliensis* (Am. Mus. 20167) was picked up in the Irdin Manha formation, but the exact locality was not recorded. Figure 794 shows the type specimen in comparison with a small individual of *Protitanotherium grangeri* (Am. Mus. 20168) from the Irdin Manha formation. Although the teeth of *M. mongoliensis* (p_4, m_1) are only slightly less elongate (ap. 43 mm.) than the corresponding teeth of *P. grangeri* (ap. 45 mm.), the transverse measurements shown in Figure 794, A, B, indicate that the *M. mongoliensis* type belongs to a relatively longer and narrower dental series than that of *P. grangeri*. This elongation of the grinding teeth is one ground for the reference of this diminutive specimen to the Dolichorhininae. More detailed comparative measurements are as follows:

Comparative measurements of species of Metarhinus and Protitanotherium, in millimeters

	M.? mongoliensis, Am. Mus. 20167 (type, fragment of jaw)	P. grangeri Am. Mus. 20168 (fragment of jaw, referred)
Linear space occupied by fourth inferior premolar and first molar (p_4, m_1)	43	45
P_4, ap. by tr	19×11	21×14
P_4, index	58	67
M_1, ap. by tr	24×14	24×17
M_1, index	58	70

Specific characters.—Of smaller size than *Protitanotherium grangeri;* inferior grinders relatively longer and narrower; valleys of posterior lobes of m_1 deeply cupped, with elevated internal border; valleys of anterior lobes open, without internal cingulum; entoconid of p_4 depressed, of m_1 elevated; depth of mandibular ramus, at interval between p_4 and m_1, 46 millimeters; thickness of mandibular ramus below same interval, 26 millimeters.

TITANOTHERES OF EASTERN EUROPE

The above description of upper Eocene and lower Oligocene titanotheres discovered in Mongolia suggests comparison with the three species of titanotheres described from eastern Europe, as follows:

1876. *Brachydiastematherium transilvanicum* Böckh and Maty, found in the neighborhood of Andrásháza (Siebenbürgen), Transylvania, southeastern Hungary, "am linken Ufer des Nádosbaches." Resembles *Protitanotherium* in size.

1892. *Menodus? rumelicus* Toula, Kajali, found northwest of Burgas on the Jambol-Burgas Railroad, eastern Rumelia. Resembles *Protitanotherium* or *Brontops* in size.

1913. *Titanotherium bohemicum* Kiernik, locality somewhat doubtful, attributed to "Süsswasserkalke von Tuchořitz oder diesen entsprechende Bildungen." Resembles *Menodus* (= *Titanotherium*) *giganteus* in size.

Brachydiastematherium transilvanicum Böckh and Maty.—In the main part of this monograph, relating to the upper Eocene titanotheres of the Rocky Mountains, *Brachydiastematherium transilvanicum* has already been compared with *Protitanotherium superbum* of the Uinta formation (*Diplacodon* zone or level C) of Utah. There is nothing new to be added as to this Transylvanian species, which is fully figured and described therein.

Menodus? rumelicus Toula.—The type of this Rumelian species (cast Am. Mus. 17602 from original in the National Museum of Vienna) is probably referable to *Protitanotherium* or to *Brontops* rather than to any species of *Menodus*. This new generic reference is based on the relatively short and broad measurements of the third inferior molar of the right side, which constitutes the type, namely, anteroposterior, 94 millimeters; transverse, 44 millimeters; index, 47; accordingly the breadth-length index of m_3 is much greater than that of the typical *Menodus*.

Corresponding with the short, broad proportions and closed valleys of the type molar of *M. rumelicus* is the paratype second inferior molar m_2 (cast Am. Mus. 17603, from original in the Vienna Museum), in which the measurements are as follows: Anteroposterior, 79 millimeters; transverse, 44 millimeters; index 56. We are therefore inclined to refer the *Menodus? rumelicus* of Toula either to *Protitanotherium* or to *Brontops rumelicus;* the latter generic reference being made more probable by the discovery of the brachycephalic *Brontops gobiensis*.

Titanotherium bohemicum Kiernik.—The type of this Bohemian species (fig. 795, C), represented in the American Museum collection by a cast (Am. Mus. 14449), is possibly referable to *Menodus* (= *Titanotherium*), although the molar proportions of the third inferior molar are intermediate between those characteristic of the brachycephalic *Brontops* and of the true dolichocephalic *Menodus*. The imperfect third inferior molar of the right side, which constitutes the type of *Menodus* (= *Titanotherium*) *bohemicum*, is

relatively less elongate than in the typical *Menodus giganteus* of South Dakota. It is also inferior in size and relatively less elongate than the type of *Menodus mongoliensis* of the Gobi Desert, described and figured above. The estimated measurements are as follows: Anteroposterior, 116 millimeters; transverse, 52 millimeters; breadth-length index, 45. The very pronounced external cingulum is comparable with that of the typical *Menodus*, but the breadth-length index shows that it is relatively shorter and broader than the extreme type of *Menodus*, such as *Menodus mongoliensis*.

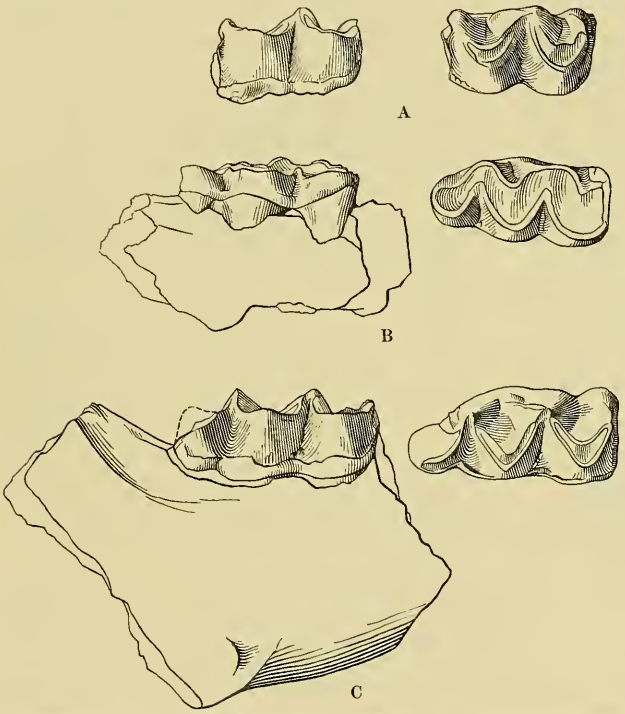


FIGURE 795.—Titanotheres of Rumelia, in the Balkan Peninsula; of Transylvania, in southeastern Hungary; and of Bohemia

A, Paratype of *Menodus? rumelicus* Toula, 1892, pp. 6–8, figs. 3, 4. Second inferior molar of the right side. Length 80 millimeters, breadth 42 millimeters, height 32 millimeters. Discovered at Kajali, the same locality as that of the type (B), but belonging to a different individual. After cast, Am. Mus. 17603.

B, Type of *Menodus? rumelicus* Toula, 1892, pp. 5–8, figs. 1, 2. Third lower molar of the right jaw, discovered near Kajali, northwest of Burgas on the Jambol-Burgas Railroad, eastern Rumelia. After cast (Am. Mus. 17602) from original in the National Museum of Vienna. Length 93 millimeters, breadth 43 millimeters; described by the author as closely resembling in its dimensions *Menodus* (*Titanotherium* or *Brontotherium*) *proutii* Leidy. Toula described in 1896 (p. 922, fig. 3) a symphysis of the lower jaw from the same locality, referring it to the same species, *Menodus? rumelicus*.

C, Type of *Titanotherium bohemicum* Kiernik, 1913, pl. 63, figs. 1–4. Fragment of right lower jaw containing m_3. Original in National Museum of Prague; cast, Am. Mus. 14449. Locality somewhat doubtful; attributed (op. cit., p. 1223) to "Süsswasserkalke von Tuchořitz oder diesen entsprechende Bildungen." Distinguished as follows (p. 1219): "Die Begründung der neuen Spezies beruht also nicht auf der Verschiedenheit in der Provenienz der europäischen Funde, sondern auf den tatsächlichen Unterschieden in den Dimensionen und der ganzen Beschaffenheit des Zahnes." Length 109 millimeters, breadth 50 millimeters.

All one-third natural size. Compare type of *Brachydiastematherium transilvanicum* Böckh and Maty, found in the neighborhood of Andrásháza (Siebenbürgen), Transylvania, southeastern Hungary, "am linken Ufer des Nádosbaches." (See Pl. LXX and fig. 100 of the present monograph.)

SURVIVING EMBOLOTHERES OF MONGOLIA

The Oligocene titanotheres of Mongolia described and figured above are those discovered in the seasons of 1922 and 1923. The seasons of 1924 and 1925 closed with the discovery of two new and highly fossiliferous Oligocene horizons, the Ulan Gochu and the Baron Sog. The fossil fields were shut off by civil war in 1926 and 1927. In 1928 extensive collections were made, establishing the overlying Baron Sog formation as a rich baluchithere horizon, with titanotheres nearly extinct, and the underlying Ulan Gochu formation as rich in the giant surviving titanotheres herewith described as embolotheres.

Subfamily EMBOLOTHERIINAE Osborn, 1929[1]

One of the most surprising results of the Fifth Central Asiatic Expedition, of the season of 1928, under the leadership of Roy Chapman Andrews and Walter Granger, was the discovery of an entirely new type of titanothere, to which the generic name *Embolotherium* is given in reference to the unique structure of the forward portion of the cranium. The name is derived from the Greek ἐμβολή, "battering ram."

As the brontothere used its horns in tossing, the embolothere used its horns for battering, assaulting, attacking, charging, and tossing. Hence the name "battering-ram-nosed titanothere" seems appropriate. From the front part of the face there arises a completely novel single bony horn composed of elongated and uplifted nasal bones; these bones are supported on a firm base of the frontals and maxillaries. In the genotypic species, *Embolotherium andrewsi*, the nasal horn rises to a height of 28 inches (fig. 797, C) and expands very broadly at the summit into a rugose bony prominence, on the under surface of which is an upward extension of the anterior nares. This single nasal protuberance is totally different in structure from the paired frontonasal bony horns of all previously known titanotheres, as shown by comparison with the frontonasal horns in the juvenile skull of *Brontops brachycephalus* (fig. 385, p. 453) or in the adult skull of *Brontotherium platyceras* (figs. 457–460, pp. 551, 552; Pl. CLXXXIX). This profound structural difference was not realized until the juvenile skull of *E.*

[1] Osborn, H. F., *Embolotherium* gen. nov. of the Ulan Gochu, Mongolia: Am. Mus. Novitates No. 353, 20 pp., May 30, 1929.

andrewsi revealed this wide contrast between *Embolotherium* and *Brontotherium*.

The subfamily Embolotheriinae, typified by the characters observed in three distinct species of *Embolotherium*, probably represents a purely Asiatic phylum, no members of which have thus far been discovered in North America; nor do the three species of *Embolotherium* from the Ulan Gochu formation here described seem to be related to the titanotheres discovered in the three older geologic formations described above (pp. 903–941, figs. 773–795); they appear rather to represent immigrants into the central Gobi region, whose ancestors lived farther north in central Asia. The geologic age of the Ulan Gochu formation is probably lower to middle Oligocene. It is intercalated between the Tertiary formations shown on page 903 as follows:

New theoretic sequence (1929) of middle Oligocene to upper Eocene formations

[Compare p. 903]

Formation	Estimated thickness	Geographic region	Life zone	Probable or estimated age
	Feet			
Baron Sog	35	Uliassutai trail	Baluchitherium n. sp	Lower and middle Oligocene.
Hsanda Gol	3, 000	Eastern Altai	Baluchitherium grangeri zone	Do.
Houldjin	30	Iren Dabasu Basin	Baluchitherium grangeri? zone	Do.
Ulan Gochu	132–195	Uliassutai trail	Embolotherium andrewsi zone; E. loucksii, E. grangeri.	Extinction of titanotheres.
Ardyn Obo	500	do	Brontops gobiensis zone; Menodus mongoliensis.	Lower Oligocene.
Shara Murun	500	do	Protitanotherium mongoliense zone; Dolichorhinus, Telmatherium, Manteoceras.	Summit of Eocene. Titanotheres very abundant.
Irdin Manha	40–100	Iren Dabasu Basin	Protitanotherium grangeri zone. Dolichorhinus olseni, Telmatherium berkeyi.	Upper Eocene. Titanotheres present.

Materials.—In all 14 individual specimens of *Embolotherium* were found in the Ulan Gochu formation associated with the remains of lagomorphs and other rodents, carnivores, creodonts, hyaenodonts, rhinocerids, lophiodonts, entelodonts, characteristic of lower to middle Oligocene age. As exposed in three sections (north of the bluffs on the Sair Usu-Kalgan trail, lat. 42° 31′ N.) by Granger and Spock, the Ulan Gochu formation shows a thickness of 132 feet at Twin Oboes, 195 feet at Urtyn Obo, and 190 feet at Holy Mesa, thus representing a long period of geologic time.

Genus EMBOLOTHERIUM Osborn, 1929

Genotypic species *Embolotherium andrewsi* Osborn, 1929

Generic characters.—Premaxillaries elongate (*Embolotherium grangeri*), reduced (*E. andrewsi*); elevated anterior bony protuberances or nasal horns expanded at the summits, moderately broad (*E. loucksii*), extremely broad (*E. andrewsi*); frontals normal, not entering into nasal protuberances. Broad postorbital expansion of vertex; zygomata extremely broad. Premolars with prominent tetartocones and partly separate metalophs; M 3 with prominent hypocone (*E. andrewsi*).

Embolotherium loucksii Osborn, 1929

Type: Am. Mus. 21610, Figure 797, A. Premaxilla elongate, nasal protuberance with upward and forward curvature arising from middle portion of vertex and directly above orbit, straight superior border relatively narrow at summit. Known from type specimen only.

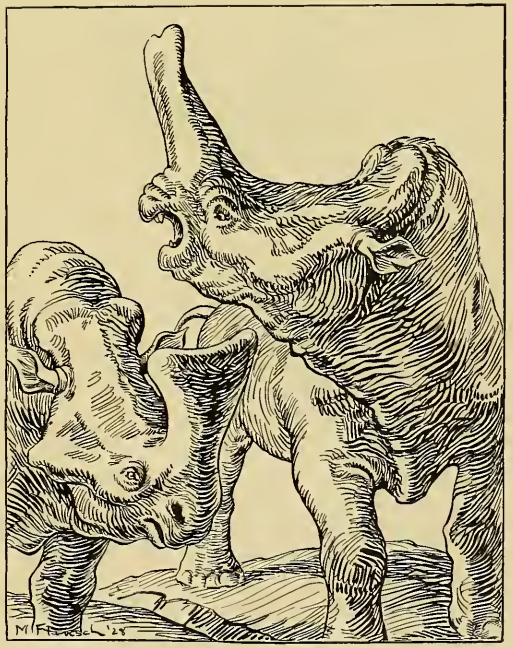


FIGURE 796.—Restoration of *Embolotherium andrewsi*, the giant single-horned titanothere of the lower to middle Oligocene of the Gobi Desert, Mongolia. Reconstructed from three crania, without knowledge of the limb skeleton. About one-thirtieth natural size

Embolotherium grangeri Osborn, 1929

Type: Am. Mus. 26002, Figure 797, B. Maxillo-premaxillary rostrum elongate, nasal bony horn extending upward and forward, slightly recurved on lower surface, with convex superior border, arising

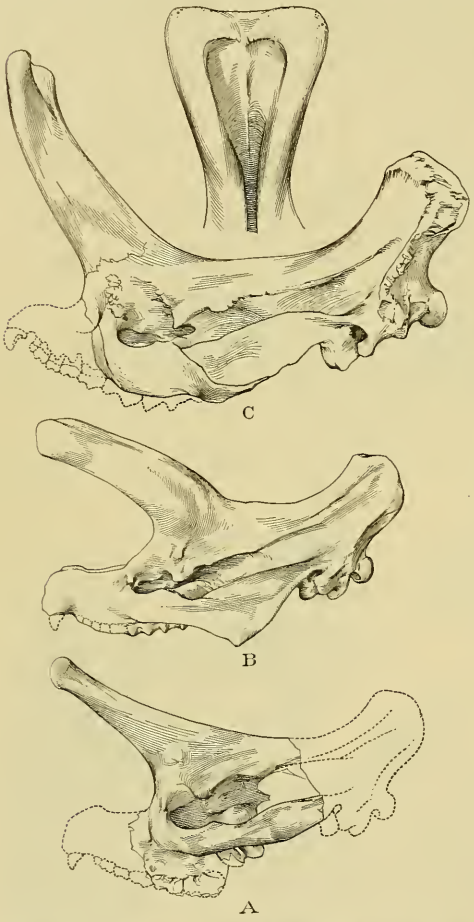


FIGURE 797.—Crania of three species of *Embolotherium*

A, *Embolotherium loucksii*, type cranium (Am. Mus. 21610), with straight, obliquely vertical, and narrow horn; B, *Embolotherium grangeri*, type cranium (Am. Mus. 26002), with elongate rostrum and central nasal horns; C, *Embolotherium andrewsi*, genotypic species, type cranium (Am. Mus. 26001). All one-tenth natural size.

from mid-cranium somewhat posterior to orbit. Zygomatic arches very broad; summit of nasal protuberance moderately broad. Known from the type and other individuals found in the upper levels of the Ulan Gochu formation.

Embolotherium andrewsi Osborn, 1929

Type: Am. Mus. 26001, Figure 797, C. Premaxillo-maxillary rostrum reduced, abbreviate, bony horns rising above and anterior to the orbit, extremely broadened at the summits, infolding nasal chamber inferiorly. Known from three complete crania and other specimens found in the upper levels of the Ulan Gochu formation.

EPILOGUE OF THE TITANOTHERE MONOGRAPH

The discovery of these great surviving titanotheres of lower to middle Oligocene age finally confirms the author's theory set forth in 1900 that central Asia was the home land of the odd-toed ungulates or Perissodactyla. Here the family Brontotheriidae was nourished on the fertile uplands of the Gobi. This grandeur heralded the oncoming period of extinction in lower to middle Oligocene time, followed by the rise of the baluchitheres as the monarchs of central Asia.

Sic transit gloria Titanotherioideorum

HENRY FAIRFIELD OSBORN.

March 16, 1929.

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